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DIEL VERTICAL MIGRATIONS OF TWO ZOOPLANKTERS (*MESOCYCLOPS* AND *CHAOBORUS*) IN A MISSISSIPPI LAKE

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INTRODUCTION

Vertical diel migrations of plankton organisms have been studied by a number of persons. Literature reviews dealing with this problem have been published by Rose (1925), Russell (1927), Kikuchi (1930), Cushing (1951), Welch (1952), Motoda (1953), and Davis (1955).

This paper is a report on the daily vertical migrations occurring in Lake Geiger, Forrest County, Mississippi. Lake Geiger is located 12 miles south of Hattiesburg in Shelby State Park. The lake is an old stream valley, which was dammed in 1943. The surface area is 320 acres and the maximum depth is 5 meters. The lake is fed by 2 small streams and has a water shed area of approximately 15 square miles.

Acknowledgments are extended to Mr. James S. Carpenter for his assistance with the field work, to Mr. Alan Stone of the U. S. Department of Agriculture for the identification of the *Chaoborus*, to the Mississippi Game and Fish Commission for the use of a boat, motor, and truck, and to Dr. J. Fred Walker, for interest in and support of the project.

METHODS

On August 25, 1958, starting at 12:00 noon a vertical series of plankton samples was taken every 3 hours until 12:00 noon of the following day. Plankton samples were taken with a 10-liter Juday plankton trap having a #20 mesh silk net. In order to minimize the possibility of zooplankters avoiding the trap, closure was effected as quickly as possibly once the trap reached the desired depth. Plankton samples, as well as water samples for oxygen analysis and temperature recordings, were taken at depths of $\frac{1}{2}$, $1\frac{1}{2}$, 3, and 4 m at a point about in the middle of the lake where the depth was $4\frac{1}{2}$ m. All samples were taken from a skiff and the sampling location was marked by a buoy. Water samples for oxy-

gen determination were collected with a Hale water sampler and analysis by the unmodified Winkler method was completed on shore within 30 minutes of the collecting time.

Regular plankton samples were taken at Lake Geiger through the latter part of the summer of 1958 so that a time for the 24-hour sampling series could be selected when the concentration of copepods was fairly high. Two copepods were present in fairly large numbers in the 24-hour series of samples. These were *Mesocyclops edax* and *Diaptomus mississippiensis*. *Mesocyclops* was by far the more numerous, comprising 84% of the adult copepod population, and its vertical movements are described below. *Diaptomus* was not abundant enough to permit a description of its vertical distribution. Large numbers of the larva of the midge *Chaoborus albatus* were present and its vertical migrations will accordingly be described.

Comments on method of presenting data

Pennak's (1943) quartile curve method is a lucid and, therefore, desirable method of depicting these migrations; however, 2 modifications of the method have been applied. The first modification takes into account the diel variation in planktonic numbers, which is considerable and regular for the 2 animals treated here. Both *Mesocyclops* and *Chaoborus* were more numerous in the water column samples during the night than during the day. Since the water column was sampled down to a depth of 4 m where the depth is $4\frac{1}{2}$ m, it is assumed that the majority of these animals were either in the mud or in the water very close to the mud-water interface; that is, within $\frac{1}{2}$ m of the mud-water interface, during the day. In the first case, the animals would be benthic; in the second, hypoplanktonic. It is apparent that the delimitations of the adjectives, hypoplanktonic, planktonic, and even-benthic are rather indefinite

Accordingly, it is assumed that the population was most completely sampled when the largest number of individuals was taken in the sampling procedure. This was at 3:00 AM for *Mesocyclops* and at 12:00 midnight for *Chaoborus*. When the number of individuals collected in the water column was only about $\frac{1}{3}$ of the maximum collected, as it was for *Mesocyclops* at 6:00 PM for instance, it is assumed that $\frac{2}{3}$ of the population was located below 4 m either in the water just above the mud or in the mud, and the first, 2nd, and 3rd quartile depths are calculated accordingly. In this case, then, the 50% quartile would be plotted as occurring below 4 m (Fig. 3). A consideration of the validity of this modification is given in the discussion.

A second modification of Pennak's method is introduced here to permit the determination of the first, 2nd, and 3rd quartile depths on the basis of a series of concentrations at regular depth intervals. The actual depth intervals employed in sampling were irregular, but a series of concentrations at regular depth intervals may be obtained by interpolation. In order to do this, the actual number of individuals collected is plotted against depth and a curve is fitted to these points and is extrapolated to the surface and to the bottom. Using these plotted frequency distributions, the concentration (number of individuals/10 liters) is tabulated for each $\frac{1}{4}$ m depth interval. The quartile depths may then be determined from a cumulative frequency column and plotted as seen in Figures 3 and 4.

RESULTS

Physical-chemical conditions

The temperature and dissolved oxygen plots as well as the Secchi disc reading are given in Figure 1. It may be seen that the lake is stratified with an oxygen-deficient zone even though the temperature decrease with depth is small, only 4°C.

The 2 oxygen curves represent maximum and minimum saturation values during the 24-hour period. The maximum curve was recorded at both noon and 3:00 P.M. and the minimum occurred at 6:00 AM. During the afternoon, additional oxygen determinations were made at 2 and 2½ m, and the concentrations entered in the maximum curve. No additional determinations were made during the period of oxygen minimum. It has been assumed that the minimum curve would follow the general pattern of the maximum curve between 1½ and 3 m. This assumed distribution is indicated by a curved line.

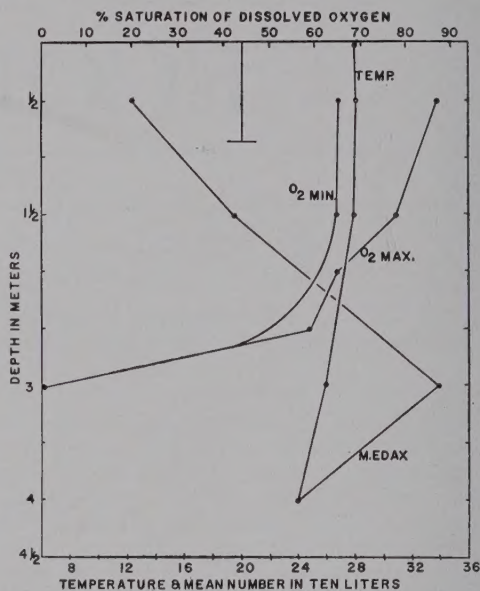


FIG. 1. Distribution of temperature and oxygen (maximum and minimum) and average distribution of *Mesocyclops edax* for a 24-hour period, Aug. 25-26. The Secchi disc level is also shown.

The average vertical distribution of *Mesocyclops edax* for the 24-hour period has been calculated by averaging the concentrations for each sampled depth and is included in Fig. 1.

Vertical movements

Two methods are employed to depict the vertical movements; one, variations in the total limnetic concentrations, are plotted for the 24-hour period to show the extent to which the population moves into the water column at night and then down to the bottom and out of the sampled water column during the day (Figs. 2 and 5), and 2, the quartile curve method with the modifications previously discussed is used to illustrate the variations in vertical distribution of the total population during the 24-hour period (Figs. 3, 4, 6).

Figure 2 shows that the *Mesocyclops* are more numerous than the *Chaoborus* and that this cyclopoid has a somewhat greater tendency to move in and out of the water column during the 24-hour period.

A diel variation in planktonic numbers is well established for *Chaoborus* larvae, which, with the exception of the recently hatched ones, normally occur in the bottom muds during the day (Juday 1921, Eggleton 1931, Wood 1956). A diel varia-

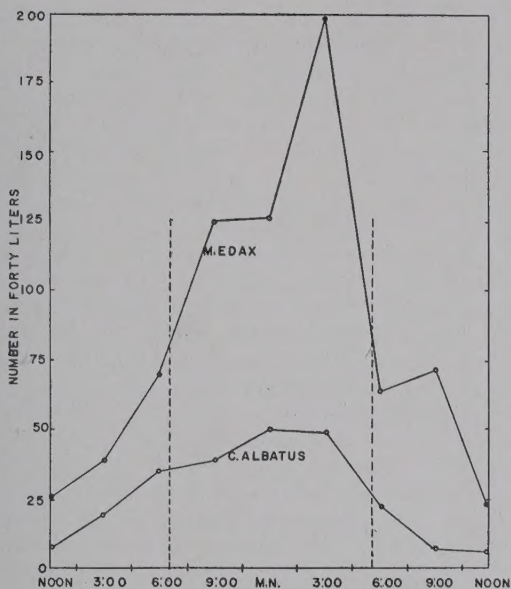


FIG. 2. Diel variations in planktonic numbers of *Mesocyclops edax* and *Chaoborus albatus* in Lake Geiger, Mississippi, based on 10-liter trap samples taken at depths of $\frac{1}{2}$, $1\frac{1}{2}$, 3 and 4 m at 3 hour intervals from noon Aug. 25 to noon Aug. 26. The vertical dashed lines show the times of sunset and sunrise.

tion in planktonic numbers of copepods is, on the other hand, a phenomenon which occurs in some instances, but not in others. Some workers (Worthington 1931, Southern and Gardiner 1932, Clarke 1934, Worthington and Ricardo 1936) have recorded it and discussed its probable meaning; others (Plew and Pennak 1949) have shown it in some of their raw data, but have not commented on it.

This tendency to move in and out of the water column may be expressed quantitatively by determining the percentage of the total limnetic population which is planktonic during the day. This percentage has been calculated by using the maximum number collected as 100% and the day time numbers are an average of the six daytime collections. On this basis, 25% of the entire adult *Mesocyclops edax* population is planktonic (i.e., found at 4 m or above) during the day and 32% of the *Chaoborus albatus* population is planktonic during the day.

It should be noted that these percentages are based only on plankton samples and do not take into account the animals which may be benthic for the entire 24-hour period. In the case of *Chaoborus*, a large percentage of the population apparently does not enter the water column during the 24-hour period (Wood 1956, Juday 1921).

An actual comparison of benthic and planktonic numbers has apparently never been made for *Mesocyclops*.

The vertical movements of *Mesocyclops edax* and the larva of *Chaoborus albatus* are illustrated in Figures 3 and 4. It is evident that there is an extensive upward movement of the populations at night and that the upward movement is more extensive for *Chaoborus* than for *Mesocyclops*. In both cases, the ascent is more gradual than the descent. This feature of the movement may be a result of the fact that the sky was completely overcast all during the afternoon of August 25, 1958, and then was clear on the morning of August 26. Not only was the sky completely overcast on the afternoon of the 25th, but there were frequent showers from noon until 8:00 PM, when the weather cleared.

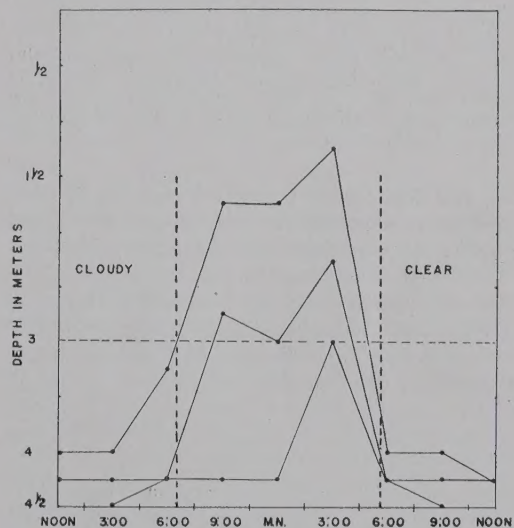


FIG. 3. Diel vertical migration of *Mesocyclops edax* illustrated by the quartile curve method. The vertical dashed lines show the times of sunset and sunrise. Below the horizontal dashed line the water is deficient in oxygen.

Mesocyclops edax (S. A. Forbes)

Only adult *Mesocyclops edax* are considered in this report. The population was made up very predominantly of adults. The few immature individuals present were early copepodids and were, therefore, easily distinguishable from the adults.

M. edax showed a striking increase in planktonic numbers at night (Fig. 2) with the maximum concentration occurring at 3:00 AM, when 198 mature individuals were taken in the 40 liters of sampled water. At noon on August 25 the same sampling procedure produced only 26 indi-

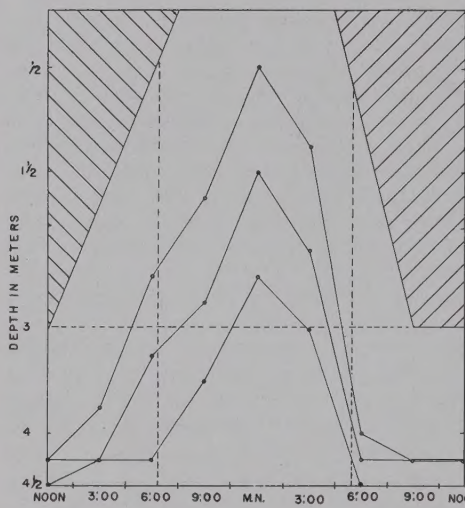


FIG. 4. Diel vertical migration of *Chaoborus albatus* in Lake Geiger, Mississippi, from noon of Aug. 25 to noon of Aug. 26. See Fig. 3 for an explanation of the dashed lines. The shaded areas indicate a complete absence of individuals.

viduals, and at noon on August 26 only 23 were obtained. The females, which constituted 80% of the mature population, were largely responsible for this pattern.

At 3:00 AM 160 females were taken. At 12:00 noon, August 25, the same sampling procedure produced only 5 females, and at 12:00 noon, August 26, 15 females were planktonic in the 40 liters of sampled water (Figure 5). Females with ovisacs numbered 41 at 3:00 AM, while none were taken in the water column at noon on either day. The males showed a maximum concentration of 41 at midnight and a concentration of 21 and 8 at the 2 noon samplings.

Therefore, all adult categories of this species are planktonic at night, but during the day they all show some tendency to be either benthic or hypoplanktonic. This tendency is quite pronounced in the females with ovisacs, which are virtually absent from the water column during the day. Non-ovigerous females exhibit the tendency to a lesser extent and the males show it only slightly. Using the same procedure as was employed above for percentage calculations, less than 1% of the ovigerous females are planktonic during the day. The non-ovigerous females are 20% planktonic and the males 60% planktonic during the day.

Although *M. edax* is usually looked upon as limnetic species (Coker 1943, Ward and Whipple 1959), Cole (1955) has shown that it is an im-

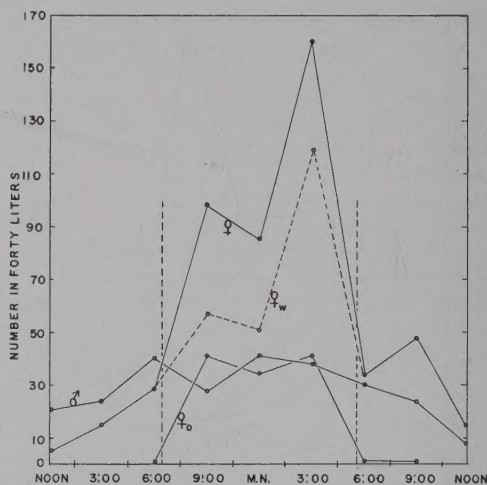


FIG. 5. Diel variations in planktonic numbers of the males (♂), all females (♀), females with ovisacs (♀o) and females without ovisacs (♀w) in the *Mesocyclops edax* population. The vertical dashed lines show the times of sunset and sunrise.

portant part of the microbenthic fauna of 2 Minnesota lakes; Crystal Lake with a maximum depth of 12.5 m and Itasca Lake with a maximum depth of 13 m. Therefore, it seems probable that *M. edax* would occur at the bottom in Lake Geiger. Apparently, Cole's work represents the only record of *M. edax* as a component of the benthic fauna. Since, however, the lacustrine microbenthos is a poorly known fauna (see Cole 1955), *M. edax* may be much more common on or in lake bottoms than is commonly supposed.

The vertical distribution of the adult *M. edax* population during the 24-hour period is shown in Figure 3. This figure also shows the population concentrated near or on the bottom during the day with a pronounced upward movement at night. There is a slight indication of midnight sinking and then a rather definite rise at 3:00 AM when the *Mesocyclops* population was highest in the water column. This 3:00 AM rise occurred too early to be attributed to pre-dawn light. The moon, which was nearly full (82% illuminated), set at 2:52 AM. It seems possible that the 3:00 AM rise could be a response to this decrease in light intensity. However, such a hypothesis does assume an extremely acute sensitivity to changes in light intensity on the part of the copepods. By 6:00 AM about 30 minutes after sunrise, the bulk of the population was found below 4 m.

The data for *M. edax* were further analyzed to determine whether or not there was a difference

in the migration pattern of the sexes. Using the maximum concentrations encountered as a measure of the population, males constituted 20% and females 80% of the population. The gravid females constituted about 28% of the female population. Figure 6 shows the Q_2 for the males, the Q_2 for all females, and the Q_2 for ovigerous females. It may be seen that the males ranged somewhat higher in the water than the females, especially from late afternoon until midnight. The median depths of the 2 sexes coincided only at midday and at 3:00 AM. The phenomenon of midnight sinking, which was only slightly in evidence for the entire adult population, was seen to occur rather definitely in the female population and not at all in the male population segment. The Q_2 of the gravid females shows that they moved higher in the water than did the female population as a whole. It is also evident that during the day the gravid females were on the bottom. In fact, a female with ovisacs was not even encountered in the samplings until 9:00 PM, at which time, however, they were well up in the water column. They remained in the water column at least until 3:00 AM, but by 6:00 AM were virtually gone. One individual was encountered at 6:00 AM and one at 9:00 AM. Both of these were at 4 m. At 12:00 noon there were none.

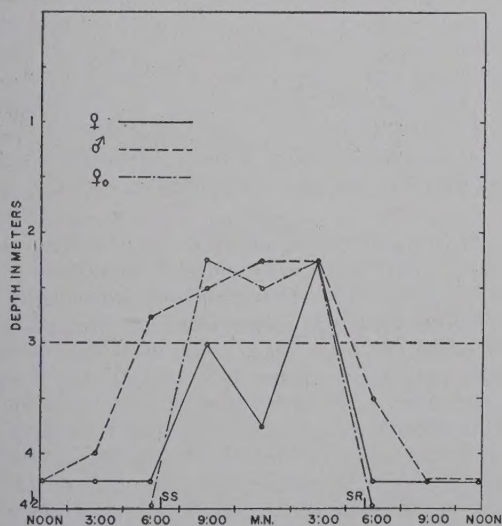


FIG. 6. Diel vertical migrations of the males (δ), all females ($\varnothing$) and females with ovisacs ($\varnothing_o$) in the *Mesocyclops edax* population in Lake Geiger, Mississippi, from noon of Aug. 25 to noon of Aug. 26. Only the 50 percentile curves (Q_2) are shown. Below the horizontal dashed line the water is deficient in oxygen. The times of sunset (SS) and sunrise (SR) are indicated on the abscissa.

During the sampling period, no dissolved oxygen was detected at 3 m or below. The dashed line at 3 meters in the figures, then, shows the maximum depth for oxygenated water. However, since the unmodified Winkler method was used, those water samples which showed no dissolved oxygen may actually have contained a small amount (See Deevey 1941, Ruttner 1953). The following discussion of conditions in O_2 -free water should be interpreted in accordance with this possibility.

An examination of Fig. 3 shows that a sizable fraction of the population was found in the O_2 -free waters throughout the 24-hour period, and that during the daylight hours the vast majority of the population was found only in the O_2 -free waters. A question which naturally arises is how long can these animals survive in O_2 -free water? Do they stay in the O_2 -free water all day or do they make occasional quick trips up into the oxygenated water? These are questions which we are really not prepared to answer, but a simple experiment was run to obtain an estimate of how long *Mesocyclops edax* might live in O_2 -free water.

At 10:30 AM on September 27, 1958, water samples were obtained from the O_2 -free water at 4 m in Lake Geiger and placed in two 250 ml glass-stoppered bottles. A plankton sample was also obtained at this depth and 3 female *M. edax* with ovisacs were placed, by means of a pipette, in each bottle, which was then carefully stoppered. The water temperature at the sampled depth was 24.6°C. This temperature was maintained fairly well with a water bath. At noon of the same day, the animals were placed in complete darkness. After 6 hours, the bottles were uncovered and all 6 animals were found to be alive. They were re-covered and left for another 6 hours, after which all of the animals were dead. From this simple experiment, it would appear that *M. edax* can survive in oxygen-free water for at least 6 hours, but not over 12 hours.

Chaoborus albatus Johnson

As may be seen in Figure 4, some *Chaoborus albatus* larvae were present at a depth of 4 m throughout the 24-hour period. *Chaoborus* were present at 3 m from 3:00 PM until 6:00 AM, at 1½ m from 6:00 PM until 3:00 AM, and at ½ m from 9:00 PM until 3:00 AM. At midnight the maximum concentration of *Chaoborus* occurred at ½ m and near maximum concentrations occurred at 1½ and 3 m. At 6:00 PM, 9:00 PM, and 3:00 AM definite maxima occurred at 3 m.

At all other times the maximum planktonic concentration was at 4 m.

Measurements of *Chaoborus* larvae reveal that the behavior varies with the length or size. The larvae were separated into 2 groups; small (1.4-3.4 mm) and large (3.5-8.0 mm). The separation at 3.5 mm, although necessarily somewhat arbitrary, is based upon a behavioral difference.

Figure 7 shows the diel variations in planktonic numbers and Figure 8 shows the vertical migrations for these 2 size groups. It may be seen that the small larvae were present in the plankton throughout the 24-hour period and showed maxima in planktonic numbers at 6:00 PM and 6:00 AM with minima during the day and during the night. A consideration of the vertical distribution (Fig. 8) shows that the small larvae moved significantly up into the water column only in the late afternoon and early evening. The 6:00 AM maxima in planktonic numbers was due almost entirely to a concentration at 4 m.

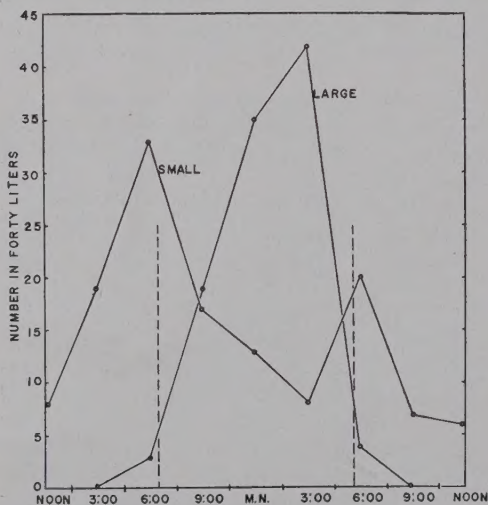


FIG. 7. Diel variations in planktonic numbers of small (1.4-3.4 mm) and large (3.5-8.0 mm) larvae of *Chaoborus albatus* in Lake Geiger, Mississippi, from noon of Aug. 25 to noon of Aug. 26. The vertical dashed lines show the times of sunset and sunrise.

The large larvae were planktonic only from 6:00 PM until 6:00 AM and exhibited a well-defined peak in planktonic numbers from midnight to 3:00 AM. Figure 8, depicting the vertical migrations, shows that the major upward movement of the large larvae occurred after 9:00 PM and, therefore, at least $2\frac{1}{2}$ hours after sunset. The population was highest in the water at midnight and 3:00 AM.

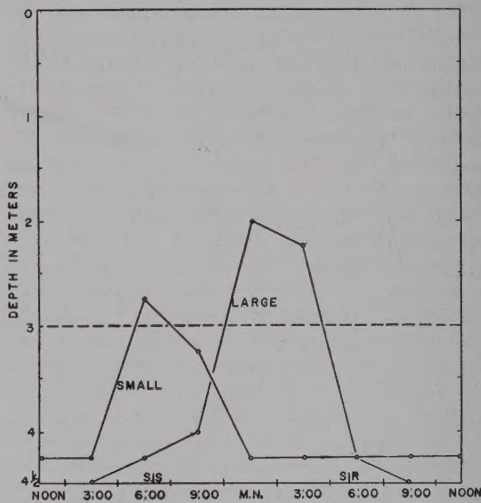


FIG. 8. Diel vertical migrations of the small (1.4-3.4 mm) and large (3.5-8.0 mm) larvae of *Chaoborus albatus* in Lake Geiger, Mississippi, from noon of Aug. 25 to noon of Aug. 26. Only the 50 percentile curves (Q_2) are shown. Below the horizontal dashed line the water is deficient in oxygen. The times of sunset (SS) and sunrise (SR) are indicated on the abscissa.

It is a matter of interest to compare Figures 4 and 8 and see that when the *Chaoborus* larvae are considered as one group, they show a single regular ascent with the population being highest in the water at midnight. When the larvae are separated into 2 size groups, one sees that there are 2 ascents, one at 6:00 PM by the small larvae and another at midnight by the large larvae. By midnight, the median depth for the small larvae has dropped almost to the bottom.

DISCUSSION

Cause of a nocturnal increase in planktonic numbers

Since a numerical increase at night for various plankters has been previously noted by several workers, a comment on their explanations is in order here.

As Worthington and Ricardo (1936) and Ulyott (1939) have pointed out, 2 hypotheses have been proffered to explain this phenomenon; (1) that the planktonic numbers only appear to decrease during the day, by virtue of ability to see and, therefore, to avoid nets and traps, and (2), that the planktonic numbers do decrease during the day because a proportion of the plankters move to or very near the bottom at that time. The present authors favor, then, the 2nd hypothesis.

The idea that plankters evade the net was first proposed by Franz (1912) and has more recently been advanced by Southern and Gardiner (1926, 1932), who state that "this is probably a serious error" but that it is an error which they are unable to evaluate quantitatively. Ricker (1938) considers the idea that certain plankters can avoid capture and seems to favor it though with some reservation. He compares net catches with trap catches and concludes that, "if some *Daphnia* avoided the net, they must have avoided the trap as well, and in about the same degree." Welch (1948), commenting on the uncertainty of this possible source of error, states, "To what extent this is an error of consequence remains to be determined."

The 2nd hypothesis was initially proposed by Behrens (1914). Later, Southern and Gardiner (1926, 1932) considered the idea that the low daytime numbers result from the plankters moving down to the lowest layers and state that "the inability to sample the bottom one or two meters is a serious drawback." They do not favor this idea, however, but prefer to explain the low daytime numbers on the basis of "the ability of some of the Crustacea to avoid the net," and partly, it seems, on the basis of an irregular horizontal distribution.

Worthington (1931) questions the conclusions of Southern and Gardiner in the discussion of his findings in Lake Victoria Nyanza. He concedes that *Chaoborus* larvae may avoid a net, but has difficulty believing that small crustacea are capable of doing so. Motoda (1953) expresses a similar opinion stating that "strong swimmers" like euphausiids may avoid a net, but that for "copepods and cladocerans this surely is not the case."

Worthington (1931) concludes that "It may be therefore that the smaller day catches are due to [the fact that] the plankton of the bottom 2 meters could never be caught; i.e. that during the day a proportion of the plankton settled on or very near the bottom." In a later paper Worthington and Ricardo (1936) give more credence to the idea of plankters avoiding capture in their discussion of sources of error, but continue to account for observed differences in day and night numbers by assuming that the animals have moved out of the sampled water column. For Lake Naivasha they state that for both *Moina* and *Cyclops* "the catches were much larger at night than in the day, which suggests that many individuals had resorted to the extreme bottom during the daylight."

Clarke (1934), commenting on the absence of *Calanopia americana* from the water column at

midday, states that "the animals were undoubtedly so close to the bottom at this time that they could not be caught by the plankton net." Pennak (1944), commenting on the fact that the plankton trap will not sample the lowermost 30 to 60 cm of water, states that "This may be a source of error in the overall diurnal migration picture, especially when a large number of organisms are restricted to the bottom meter during midday."

Cushing (1951) points out that the contention that plankters avoid the net is seriously weakened by the fact that in many studies "the animals which appear at the surface have at the same time disappeared from the lower levels."

It is, therefore, apparent that a majority of the investigators who have considered this problem have concluded that an observed daytime reduction in planktonic numbers is real and a result of the plankters having assumed either a hypoplanktonic or benthic existence during the day. Certain aspects of the present study serve as evidence for the hypothesis that the reduction in daytime planktonic numbers is real and not an artifact.

If one could select different plankters with the same ability or capacity for avoiding capture by the trap, all should exhibit the same percentage reduction in daytime numbers if this reduction was effected solely by ability to avoid the trap. If, on the other hand, the daytime reduction is real, the selected plankters would show the same percentage reduction in daytime numbers only if they all left the water column to the same degree, but if they dropped out of the water column to different extents, their percentage reductions in daytime numbers would be different. If, then, one could demonstrate this sort of difference, he could contend that the reduction is real.

The major difficulty inherent in this line of reasoning lies in fulfilling the requirements of the initial assumption, namely, that the selected plankters have the same capacity for avoiding the trap. An approach toward satisfying this assumption may be made by selecting categories in the same species. The approach may be refined by restricting the selection to the same sex and stage of the same species, for instance, adult non-ovigerous females and ovigerous females.

Mesocyclops edax has been separated into 3 adult categories, males, females without ovisacs, and females with ovisacs. The percentages planktonic during the day have been calculated above in the discussion of *M. edax*. From these figures, it may be seen that there is a 40% daytime reduction in males, an 80% daytime reduction in non-ovigerous females, and over a 99% daytime reduc-

tion in ovigerous females (also see Fig. 5). Thus, definite differences exist. It is true that the males are smaller than the females and so may not be able to swim as rapidly, but one would hardly expect a 40% difference. The ovigerous females, if anything, should be slower than the non-ovigerous females and, therefore, less capable of avoiding a trap. They were, however, virtually absent from the daytime collections, while 20% of the non-ovigerous females were present in the plankton. On the basis of these differences, then, it would appear that the observed reduction in daytime numbers is real and, accordingly, in the first modification of the quartile curve method, the reduction is treated as real.

Nocturnal increases in planktonic numbers of cyclopoids

A marked nocturnal increase in the planktonic numbers of cyclopoids is to be seen in the data of Plew and Pennak (1949) and Worthington and Ricardo (1936). Plew and Pennak (1949) present data on *Cyclops bicuspidatus* which show a movement up through the water at night. From Table I of their paper, the animals per liter on January 17 for *C. bicuspidatus* have been added for each collection time and the totals plotted against time (Figure 9) to show the variation in planktonic numbers during the 24-hour period. It may be seen that there is a marked increase in planktonic numbers at night and that the time variation of planktonic numbers of *C. bicuspidatus* is rather similar to that of *M. edax*. It should be added here that the July 19 collection of Plew and Pennak (1949) shows an entirely different picture of the diel variation in planktonic numbers of *C. bicuspidatus*, thus illustrating how this behavioral aspect can vary for the same species in the same lake at different times of the year.

Worthington and Ricardo (1936) give data on the diel variation in planktonic numbers of *Cyclops* (*Mesocyclops*) *hyalinus* in Lake Naivasha, Africa. Their data have been plotted in Fig. 9 and show maximum planktonic numbers at 6:00 AM, which was dawn.

In Fig. 9 one can compare the curves for planktonic numbers versus time for *M. edax* in Lake Geiger, Mississippi (4.5 m), *C. bicuspidatus* in an Indiana lake (14 m) and *C. hyalinus* in Lake Naivasha, Africa (17.5 m). The depth at the sampling station is given in parenthesis after the name of the lake. It may be noted that these instances of a nocturnal increase in planktonic numbers occur in fairly shallow lakes. These curves show that the increase in planktonic numbers begins in the daylight hours of the afternoon

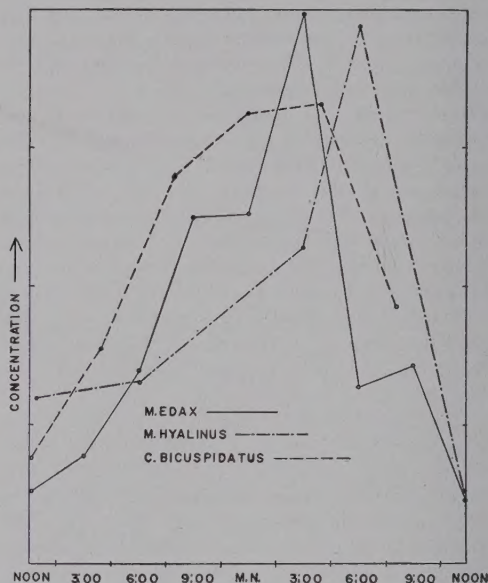


FIG. 9. Diel variations in planktonic numbers of *Mesocyclops edax* in Lake Geiger, Mississippi, in August, *Mesocyclops hyalinus* in Lake Naivasha, Africa, in February (Worthington and Ricardo, 1936) and *Cyclops bicuspidatus* in Merom Gravel Pit Lake, Indiana, in January (Plew and Pennak 1949). Concentrations are not to scale.

and is continued more or less throughout the night with a rather sudden decrease occurring at or very shortly after sunrise. Assuming that the nocturnal changes in planktonic numbers are not significantly influenced by irregular horizontal distribution, and this is probable since all 3 curves are more or less alike in regard to an increase from noon to sunrise, we see that individuals are leaving a hypoplanktonic or benthic existence and entering the sampled water column not only in the afternoon but in large numbers during the night, in Lake Geiger after midnight, in Lake Naivasha after 3:00 A.M. In the Indiana lake the nocturnal numbers increased less. These movements suggest that the extrinsic stimulus, if there is one, for the movement up through water is not light.

Accordingly, these findings are not consistent with the rather widely accepted conception that diel vertical migrations are effected by the animal's striving to remain at an optimum light intensity, but rather suggest some sort of interaction of a negative "geotropism" and a negative "phototropism" similar to that suggested by Worthington (1931). However, in this instance the supposed negative geotropism is apparently

not persistent as Worthington suggests, but is either delayed or intermittent since many of the cyclopoids do not move into the sampled water column until after midnight.

It should be appended here that some investigations have shown no significant variation in diel numbers of planktonic cyclopoids. This is the case for *Cyclops strenuus* in Lake Lucerne (Worthington 1931) in Lough Derg (Southern and Gardiner 1932) and in Lake Windermere (Ullyott 1939) as well as for *Mesocyclops leuckarti* in Lake Lucerne (Worthington 1931). The absence of a diel variation in planktonic numbers in these instances might be due to the greater depths of these lakes.

Vertical movements in the genus Mesocyclops

Vertical movements of *Mesocyclops edax* have apparently not been previously described. The vertical movements of 2 species of the genus *Mesocyclops*, as defined by Coker (1943), have been recorded. There are *M. leuckarti* in Lake Lucerne (Worthington 1931) and *M. hyalinus*, mainly in Lake Naivasha (Worthington and Richardo 1936). In both cases the data presented are for a population which is almost exclusively female.

M. leuckarti apparently showed no significant diel variation in planktonic numbers and was restricted to the surface layers in Lake Lucerne, where its daytime level was about 10 m and night time level about 5 m. Its movements were fairly typical, although "the downward movement seems to have been postponed for an hour or two after daylight."

The behavior of *M. leuckarti* in Lake Lucerne is, accordingly, quite different from that of *M. edax* in Lake Geiger. This is not surprising and could be largely attributed to the difference in depth of the 2 lakes. Lake Lucerne is 106 m deep.

As indicated above, *M. hyalinus* shows in Lake Naivasha a diel variation in planktonic numbers which is similar to that recorded for *M. edax* in Lake Geiger (see Fig. 9).

SUMMARY

The diel vertical movements of the copepod *Mesocyclops edax* and of the larva of the dipteran *Chaoborus albatus* in Lake Geiger, Mississippi, are described for a 24-hour period running from noon of August 25 until noon of August 26, 1958. Both of these plankters show a marked diurnal decrease in planktonic numbers. The diurnal planktonic populations are, for *Mesocyclops*, 25% and, for *Chaoborus*, 32% of the maximum noc-

turnal population. In the *Mesocyclops* population less than 1% of the females with ovisacs, 20% of the females without ovisacs, and 60% of the males are planktonic during the day. These differences in daytime reductions in planktonic numbers within the same species are cited as evidence that this cyclopoid is not evading the net during the day.

The majority of both populations occurred in the oxygen-deficient hypolimnion during most of the day. At night both of the populations move up into oxygenated water. Slight differences in migrations were found for the 3 categories of the *Mesocyclops* population. In the case of the *Chaoborus*, small individuals moved up into oxygenated water at 6:00 PM, whereas the upward movement of large individuals was at midnight and afterwards.

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POPULATIONS OF AMPHIBIANS AND REPTILES IN THE SUBMONTANE AND MONTANE FORESTS OF CUERNOS DE NEGROS, PHILIPPINE ISLANDS

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INTRODUCTION

Papers concerned with the herpetofauna of the Philippine Islands have been primarily taxonomic. Relatively few investigations have been concerned with the faunal communities, with the ecology of specific groups such as amphibians or reptiles, or with the nature and dynamics of populations of these animals in the tropical forest of the Philippines or immediately adjacent Pacific Islands. Some of the more useful general references and the limited Philippine papers include: Alcala and W. C. Brown (1957); W. H. Brown (1919); W. H. Brown and Mathews (1914); W. C. Brown and Alcala (1956, 1957); W. C. Brown and Reyes (1956); Cendaña and Fernin (1940); Dammernan (1948); Inger (1954, 1959); Mertens (1934); Richards (1952); Van Steenis (1957); Villadolid and del Rosario (1930).

The present study was undertaken to obtain information concerning the specific habitats, distribution in relation to forest zones and the density of populations of amphibians and reptiles on Cuernos de Negros, a 1750 meter volcanic peak, in southern Negros Island (see Figure 1).

Forest Communities

The Philippines are in a region of tropical rain forest, and Cuernos de Negros exhibits an altitudinal zonation of the forest which is quite

typical of the higher mountains throughout the archipelago. A lowland, dipterocarp forest is

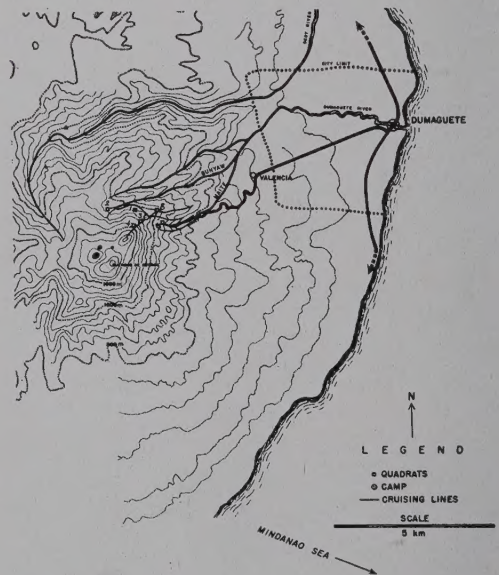


FIG. 1. Map showing Cuernos de Negros area (after AMS Map, NC51-10, Series S501) showing principal cruising lines and quadrats on the northern and eastern approaches to the north peak.

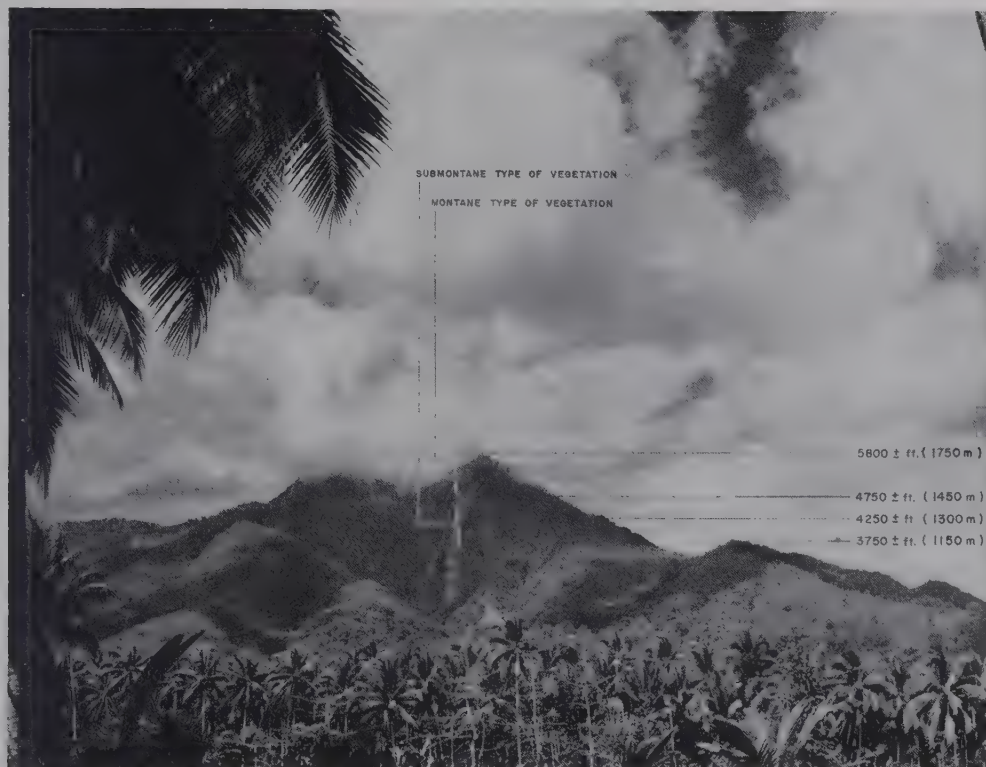


FIG. 2. Cuernos de Negros as seen from the eastern approach at an altitude of about 300 m.

present at lower altitudes, a submontane (mid-mountain of some) forest at middle altitudes and a montane (mossy of some) forest at high altitudes. The altitudes which may be designated as the upper and lower limits of the submontane and montane forests vary with such factors as latitude, height of the mountain, degree of isolation from other mountain peaks, proximity to the coast and rainfall.

On Cuernos de Negros the area from 775 or 925 to 1050 meters is more or less transitional between dipterocarp and submontane forest. More typical submontane forest occurs from 1050 to about 1325 or 1350 m. A transition to montane forest begins at about 1325 or 1350 m, and relatively typical montane forest is exhibited on the north peak above 1400 m (Figure 2). Below 775 to 925 m most of the coastal plain and lower slopes on the eastern side have long been under cultivation. As a result the typical dipterocarp forest is very poorly represented on the eastward approaches to the Cuernos de Negros, except for scattered patches along some of the streams and narrow ridges. However, dipterocarp forest does occur at lower elevations on the southern and west-

ern approaches. Patches of other types of forest communities also occur at low elevations. These include secondary growth, bamboo thicket, mangrove swamp, and beach forest.

Structurally, the dipterocarp forest is 3-storied. In this part of the Oriental Region the trees of the upper stratum (3rd story) attain heights of 22 to 45 m. The 2nd story, which forms a more solid canopy than the upper story, has an average height in this region of 16 to 18 m, while the lowest tree story has an average height of 8 to 10 m. Below this canopy is the shrub (often, mostly young trees) and herb strata. In many instances these last 3 strata tend to blend into each other to a varying extent and are not sharply defined. Large epiphytic ferns as well as other epiphytes and lianas are numerous but less dense and conspicuous than in the more humid submontane and montane forest zones.

In the submontane forest, the trees of the upper (2nd story range in height from about 14 to 22 m; those of the first story from about 6 to 12 m. Tree ferns, *Cyathea* sp., ranging from 4 to 9 or 10 m in height are numerous in this forest zone. The bird's nest fern, *Asplenium nidus* is very

conspicuous, situated on tree trunks or branches at heights from 1 to 2 to 10 or 12 m above the forest floor. Other epiphytic ferns are also present on the trunks of trees and tree ferns along with mosses, liverworts and some flowering plants. Lianas, including climbing bamboo and climbing screw pines are also numerous (Figure 3).



FIG. 3. Original submontane forest on the north slope of Cuernos de Negros at an altitude of 1050 m: (a) lower trunks of trees and ground cover, (b) crowns of trees with lianas, (c) epiphytic fern, *Asplenium nidus*.

In the one-storied montane forest, the trees range in height from 4 to 12 m. Trees, lianas and shrubs form a dense growth rather thickly cov-

ered with epiphytic bryophytes. The ground cover of bryophytes, pteridophytes and herbs is also more dense than in the submontane forest. A conifer, *Agathis alba* (Lam.) and the pitcher plant, *Nepenthes* sp. also make their appearance in this zone.

Climatically, as well as morphologically, the areas we have classified as submontane and montane forests appear to be in reasonably close agreement with those so classified by W. H. Brown (1919) on Mount Maquilang. The different latitudes of the 2 mountains as well as altitudes and variations in height above the ground at which temperatures were taken may well account for differences as great as those observed.

AREA SAMPLED AND METHODS

Area sampled

Preliminary collections of amphibians and reptiles occurring in the forested mountains in southern Negros Island were made at various locations and times from 1955 to 1957. An intensive survey of the forested areas on the northeast and north slope of the north peak of Cuernos de Negros was conducted during the period, March 22 to May 13, 1958. The field party consisted of 6 men in addition to the authors. Additional data on the dipterocarp forest were also obtained by a field party of 6 men during a 10-day period in December, 1958, in original forest at an altitude of about 600 m on the southwestern approaches to Cuernos de Negros.

Primary emphasis during the period from March to May, 1958, was on the plateau and ridges to the north and northeast of the north peak between 925 and 1125 m and the north side of the north peak between 1100 m and the summit. Our measurement of the height of the north peak, using a pocket barometer (Watrous and Co., Model 210/12) was about 1650 m. However, it is assumed that this, and other recorded altitudes above base camp (Fig. 1) are probably somewhat low since the height of the north peak on AMS map, NC 51-10, Series S501, is between 1750 and 1800 m.

Methods

Field work was conducted from a base camp in a small clearing at the edge of the submontane forest at an altitude of about 1100 m (Fig. 1). This was located in the shallow saddle at the point where the 2 ridges immediately north of the Maite River join at the base of the steep slope on the north side of the north peak.

Six quadrats of approximately 930 square meters (10,000 square feet) each (there is one

exception, quadrat number 1 is about 610 m²) were established at selected altitudes between 800 m and 1450 m, in locations that showed no evidence of having been cut over. As shown in Fig. 1, the quadrats were located as follows: 1 and 2 were in lower altitudes of the submontane forest at about 1100 m; No. 3 was in the upper submontane forest at 1275 m; No. 4 was in the lower montane forest at 1425 to 1450 m; No. 5 was in transitional dipterocarp submontane forest at 975 m and No. 6 at 800 m.

Temperature and humidity

Temperature measurements were taken for varying periods at different altitudes from late March through early May, 1958. A 3-pen portable, recording thermometer, Taylor Model X-76N317, equipped with stainless steel bulbs, one 15-foot and two 35-foot capillary systems was used. The instrument was installed for a period of 2 weeks in late April at an altitude of about 1050 m in the submontane forest on the edge of the south bank of the Bunyaw River ravine and for one week in May in the Montane forest on the steep slope of the north side of the north peak of Cuernos de Negros at an altitude of about 1450 m. This instrument did not prove wholly satisfactory under the field conditions. Other periodic measurements were taken with standard laboratory and field, glass thermometers.

Humidity measurements were taken for varying periods at different altitudes during part of April and early May, 1958. The instrument used was a Friez, aspirator type, psychrometer, Model HA-2.

Faunal sampling

Both quadrat and cruising methods were used in sampling populations of amphibians and reptiles. Cruising methods alone were employed in the collecting of birds, mammals and occasional samples of some of the forest invertebrates.

In the quadrats all specimens of amphibians and reptiles observed in the area were collected in order to obtain a total count in so far as this was possible. Specimens were collected under and in duff and rotting logs or stumps, on the forest floor and in the soil. This was accomplished by removing the shrubs and herbaceous plants and digging to a depth of several inches to a foot or more in the soil. Also the large-leaved epiphytic plants, primarily ferns, were cut from tree trunks or branches and searched after being placed on ground tarps to reduce the chance of escape of any animal secreted in the roots or leaf bases. Leaf axils of other large-leaved plants in the floor-stratum, as well as those among the

lianas, were also examined for possible amphibian or reptilian inhabitants.

Cruising was carried out in original forest, secondary growth, along stream margins, in strand associations and in some cleared or semi-cleared areas between the altitudes of sea level and 1750+ m, the summit of the north peak of Cuernos de Negros, with emphasis on the area above 800 m. The same collecting techniques were used in the arboreal and soil or surface strata.

RESULTS AND DISCUSSION

Herpetofauna of the dipterocarp, submontane and montane zones

When the project was begun, 31 species (11 amphibians and 20 reptiles) were recorded for Cuernos de Negros and adjacent lowlands. We now have records of 67. These include 14 amphibians, 27 lizards and 26 snakes. Of these, 2 amphibians, 6 lizards and at least 2 snakes (*Bufo m. marinus*, *Rana c. cancrivora*, *Gekko gekko*, *Hemidactylus frenatus*, *Cosymbotus platyurus*, *Gehyra mutilata*, *Varanus salvator nuchalis*, *Emoia atrocostata*, *Cerberus rhyncops* and *Lygodon aulicus*) are, at the present time, non-forest forms in the Cuernos de Negros area, being found in beach, swamp or lowland-stream habitats, cultivated areas or in association with human habitations.

Of the remaining 57 species, 2 snakes (*Ophiophagus hanna* and *Zaocys luzonensis*) are known only from single specimens taken in cruising samples between 900 and 1200 m; one snake (*Calophis calligaster gemianulis*) from 3 specimens with insufficient data; one lizard (*Lepidodactylus herrei*) from 5 specimens partly associated with cultivated areas and partly unknown as to habitat; and 2 snakes (*Chrysopelea paradisi* and *Oxyrhabdium modestum*) known only from the environs of Dumaguete City. All but *Chrysopelea paradisi* may typically be forest inhabitants. However, they are omitted from the discussion which follows in view of the lack of adequate information about their habitats in this area.

Of the 51 species which we regard as primarily forest-dwelling forms, our knowledge of those occurring in the submontane and montane zones is based upon quadrat and cruising samples within a large tract which is completely covered by original forest. Our knowledge of the species occurring in the dipterocarp forest is more fragmentary since it is based on samples from the transitional dipterocarp-submontane forest, both original and secondary, which borders on the submontane and extends at various points from 1050 m down to about 925 m, and such additional in-

TABLE I. Amphibians and reptiles inhabiting the dipterocarp, submontane and montane forests on Cuernos de Negros

Species	Dipterocarp	Submontane	Montane
<i>Rana erythraea</i>	x	—	—
<i>Rana e. everetti</i>	x*	x	—
<i>Rana microdisca leytenis</i>	x	—	—
<i>Rana magna visayanus</i>	x*	—	—
<i>Ooeidozoya l. leavis</i>	x*	—	—
<i>Cornufer corrugatus</i>	x*	—	—
<i>Cornufer guentheri</i>	x*	x **	—
<i>Cornufer hazelae</i>	x* †	x	x
<i>Cornufer meyeri</i>	x*	x	x
<i>Rhacophorus leucomystax quadrilineatus</i>	x	—	—
<i>Rhacophorus p. pardalis</i>	x	x	—
<i>Kaloula conjuncta negrosensis</i>	x	x	—
<i>Cyrtodactylus philippinicus</i>	x*	—	—
<i>Gekko monarcho</i>	x	—	—
<i>Lepidodactylus brevipes</i>	x*	x	—
<i>Draco volans</i>	x	—	—
<i>Hydrosaurus pustulosus</i>	x*	—	—
<i>Calotes m. marmoratus</i>	x	—	—
<i>Gonycephalus sophiae</i>	x	—	—
<i>Brachymeles gracilis taylori</i>	x*	x	—
<i>Brachymeles schadenbergi talinis</i>	x*	x	—
<i>Dasia smaragdina philippinica</i>	x	—	—
<i>Lygosoma (Leiopolisma) a. auriculatum</i>	x	x	—
<i>Lygosoma (Leiopolisma) pulchellum taylori</i>	x*	—	—
<i>Lygosoma (Leiopolisma) q. quadrivittatum</i>	x	—	—
<i>Lygosoma (Leiopolisma) rabori</i>	x*	—	—
<i>Lygosoma (Sphenomorphus) a. arborens</i>	x*	x	x
<i>Lygosoma (Sphenomorphus) jagori grande</i>	x*	—	—
<i>Lygosoma (Sphenomorphus) steerei</i>	x*	x	x
<i>Mabuya multicarinata</i>	x*	x	—
<i>Mabuya multifasciata</i>	x*	x	—
<i>Dibamus argenteus</i>	x	—	—
<i>Typhlops carlaonensis</i>	x	—	—
<i>Typhlops braconia</i>	x*	—	—
<i>Typhlops luzonensis</i>	x*	—	—
<i>Python reticulatus</i>	x	—	—
<i>Dendrelaphis boiga</i>	x	—	—
<i>Dendrelaphis terrificus</i>	x	—	—
<i>Natrix n. negrosensis</i>	x	—	—
<i>Elaphe erythrura</i>	x*	—	—
<i>Oligodon modestum</i>	x*	x	—
<i>Pseudorabdion monamarae</i>	x*	x	—
<i>Pseudorabdion montanum</i>	—	x	x
<i>Pseudorabdion ozycephalum</i>	x*	—	—
<i>Calamaria gervaisi iridescens</i>	x*	x	x
<i>Oxyrhabdion leporinum visayanum</i>	x	—	—
<i>Cyclocorus lineatus</i>	x*	x	—
<i>Psemmodynastes pulverulentus</i>	x*	—	—
<i>Dryophis preocularis</i>	x*	—	—
<i>Dryophiops philippina</i>	x	—	—
<i>Trimeresurus wagleri</i>	x*	—	—

* These species were obtained in original dipterocarp forest at an altitude of about 450 to 600 meters on the southwestern approach to Cuernos de Negros during a brief trip there in December, 1958.

† Rare

** Lower border

formation about the fauna of the earlier dipterocarp forest at lower altitudes in this region as can be gained from crusing samples in secondary growth, along the borders of clearings, and the forest patches along some of the stream areas. However, sampling over a period of 10 days in December, 1958, in original dipterocarp forest at an altitude of 600 m on the southwest side of Cuernos de Negros added no new species but

confirmed our previous findings for 30 of the 50 lowland forest species given in Table I.

As is also shown in Table I, only 20 (about 40%) of the forest species occur in the submontane zone. Six other species (*Cornufer corrugatus*, *Cyrtodactylus philippinicus*, *Lygosoma (Leiopolisma) pulchellum taylori*, *Lygosoma (Sphenomorphus) jagori grande*, *Typhlops luzonensis*, *Natrix n. negrosensis*), known for the upper transitional zone between 925 and 1050 m, may prove to range into the submontane zone at times, but have not yet been taken there. Six of the 20 (about 12% of the total forest species) extend their range into the montane zone. Only one of these, a snake *Pseudorabdion montanum* is completely restricted to the submontane-montane region. However, one amphibian, *Cornufer hazelae*, is rare in the dipterocarp zone, being replaced there by its ecological equivalent, *Cornufer guentheri*. None are limited to the montane zone.

Specific habitats of the species occurring in the submontane and montane zones

These humid tropical forests exhibit, as previously noted, a typical vertical stratification in the dipterocarp and submontane zones, complicated by numerous lianas and epiphytes, which provides varied microhabitats for arboreal amphibians and reptiles. Six of the 20 species listed for the submontane zone are primarily arboreal. These include 4 frogs, *Cornufer guentheri*, *Cornufer hazelae*, *Rana everetti* and *Rhacophorus pardalis* and 2 lizards, a gekkonid, (*Lepidodactylus brevipes*) and a skink (*Lygosoma (Leiopolisma) auriculatum*). The other 14 species, 3 frogs, 6 lizards and 5 snakes occupy the surface and sub-surface strata.

The 2 arboreal cornufers were found primarily in the leaf axils of the bird's nest fern and climbing screw pine at heights from a little less than a meter to 10 m, above the ground. A few were taken among the leaves of other epiphytes or lianas, and in the leaf axils of gabi, a very large-leaved herbaceous plant of the forest floor. Only *Cornufer hazelae* occurs in the montane zone. In this zone the climbing screw pines are more numerous and the bird's nest are usually smaller, and most specimens were taken from the leaf axils of the screw pine.

Records of either of these species being taken in any other situation are rare. Inger (1954 p. 364) notes that 3 specimens of *C. guentheri* collected in dipterocarp forest in Mindanao were found respectively on a log over a stream, adhering to a tree trunk, and on the ground. Brown and Alcala (1955 p. 100) note that several speci-

mens of *C. hazelae* were taken at night in the Mount Canlaon area on wet rocks near a stream. Eggs of both species undergo direct development and have been taken by the authors from the leaf axils of the bird's nest fern, the climbing screw pine and the gabi plant.

Racophorus pardalis was rarely observed and then only in trees growing along mountain streams or pools. In one instance, this frog was heard calling in the early evening and was collected from leaves and branches about 9 m above the ground. The next morning the foamy egg mass of this species was found attached to the leaf of a fern about one m above the pool at the base of the tree.

Lygosoma (Leiopisma) auriculatum was found only in the humus and root masses of the bird's nest fern at heights from about a meter to 10+ m above the ground in the submontane zone. Fully developed young have been found in oviducts of females. There is no evidence that eggs are ever laid.

Lepidodactylus (brevipes) has been found only in leaf axils and humus of aerial ferns in the submontane zone. Eggs, presumably of this species, have been found in the same locations. At lower altitudes, in the dipterocarp and transitional dipterocarp-submontane zones, a few specimens have been taken among leaves and in rotting logs on the forest floor as well as in aerial ferns.

Of the 3 non-arboreal amphibians, *Ooeidozyga laevis* is an aquatic frog taken only in permanent pools, usually associated with forest streams in the submontane forest area. In the lowland, cultivated areas it is found also in carabao wallows, ditches and flooded rice fields. *Kaloula conjuncta negrosensis* has been observed in large numbers in breeding congresses around pools or lakes in the lowlands and the forest up to about 900 m. At other times usually only one or a few specimens are found. On the night of May 6, 1958 a group of 8 males were taken while calling around a small pool in the lower submontane zone at about 1100 m altitude on the north peak of Cuernos de Negros. A few isolated specimens have also been collected at night from branches of forest trees on axils of leaves of wild banana plants, in the transitional dipterocarp-submontane or lower submontane zones. In the lowland cultivated area specimens have been dug out from beneath humus or from the soil around root masses of plants at various times of the year. It is probable that this species is primarily burrowing throughout its range, emerging infrequently except for breeding.

Cornufer meyeri is a forest frog living in the

duff and loose soil, beneath the moss of the forest floor, or beneath or inside rotting logs. Occasionally specimens are found in aerial ferns or moss growing on trunks of trees a foot or so off the ground. Eggs are usually deposited in duff-covered depressions or crevices in the soil. However, one clutch was found in an aerial fern growing out of a tree trunk near the ground.

Rana everetti adults are seldom seen in the daytime. One was taken in late afternoon from the low branch of a tree overhanging the Maite River in a well shaded part of the ravine at an altitude of about 350 m. Others have been collected at night in similar situations or on rocks in and on the banks of streams. Eggs and larvae have been taken in pools of forest streams and in lakes up to altitudes of 1200+ m.

Of the 11 species or non-arboreal reptiles occurring in the submontane and montane zone, 2 of the lizards, *Brachymeles schadenbergi talinis* and *Brachymeles gracilis taylori*, and 2 snakes, *Pseudorabdion montanum* and *Calamaria gervaisi iridescens*, are strictly burrowing, being found in the soil beneath logs or duff of the forest floor, or around the roots of trees. The other 3 snakes, *Cyclocorus lineatus*, *Pseudorabdion mcnamarae* and *Oligodon modestum* are found primarily in the same habitats but occasional specimens were found on the surface especially in the early hours of the day. The 2 sphenomorphid lizards, *Lygosoma (Sphenomorphus) arborens* and *Lygosoma (Sphenomorphus) steerei* were found not only beneath the duff and beneath logs or rocks but frequently during the day active on the surface. *L. arborens* is most abundant along the banks and among the rocks bordering the mountain streams and at times was observed motionless on the top of such rocks though not exposed to direct sunlight. We have occasionally seen a specimen on the exposed roots or inclined lower trunk of a tree but have not found it to be primarily arboreal as reported by Taylor (1922, p. 188). One specimen of *L. steerei* was taken from a leaf axil of a screw pine a few feet above the ground in the lower montane forest on April 24, 1958. The 2 species of *Mabuya*, *multifasciata* and *multicarinata* were seen on the surface in somewhat open areas at the lower edge of the submontane zone rather than the dense forest.

Distribution patterns and population densities in the submontane and montane zones

On the basis of the total samples from quadrats and of cruising the altitudinal limits of distribution of species within the montane, submontane

TABLE II. Results of population sampling of forest amphibians and reptiles in the transitional dipterocarp-submontane forest and secondary growth between 925 and 1050 m

Species	Quadrat 5 (929 m ² alt. 1010 m)	Cruising (alt. 925- 1010 m)	Cruising (alt. 1010- 1050 m)
<i>Rana magna visayanus</i>	0	x	—
<i>Cornufer corrugatus</i>	2	—	—
<i>Cornufer guentheri</i>	0	x	x
<i>Cornufer hazelae</i>	0	x	x
<i>Cornufer meyeri</i>	18	x	x
<i>Lepidodactylus brevipes</i>	1	x	—
<i>Cyrtodactylus philippinus</i>	0	x	—
<i>Lygosoma (Leiopisma) a. auriculatum</i>	1	—	—
<i>Lygosoma (Leiopisma) pulchellum</i> <i>taylori</i>	0	x	—
<i>Lygosoma (Sphenomorphus) arborens</i>	8	—	x
<i>Lygosoma (Sphenomorphus) jagori</i> <i>grande</i>	4	—	x
<i>Lygosoma (Sphenomorphus) steerii</i>	1	—	x
<i>Brachymeles gracilis taylori</i>	12	x	x
<i>Brachymeles schadenbergi talinis</i>	—	—	x
<i>Typhlops luzonensis</i>	0	x	—
<i>Calamaria gervaisi iridescens</i>	1	x	—
<i>Cyclocorus lineatus</i>	1	—	—
<i>Pseudorabdion menamarae</i>	1	—	—
<i>Natrix n. negrosensis</i>	0	x	—

TABLE III. Numbers of specimens obtained in sampling of forest amphibians and reptiles in the submontane forest of Cuernos de Negros

Species**	QUADRATS (929 m ²)			CRUISING***		
	No. 1* Altitude 1100+m	No. 2 Altitude 1100+m	No. 3 Altitude 1275 m	1050- 1150 m	1150- 1225 m	1225- 1400 m
<i>Ooidozygia l. laevis</i>	—	—	—	x (8)	—	—
<i>Cornufer guentheri</i>	3	1	0	x (14)	—	—
<i>Cornufer hazelae</i>	21	14	11	x (14)	x	x (7)
<i>Cornufer meyeri</i>	57	53	94	x (14)	x	x (13)
<i>Rhacophorus p. pardalis</i>	0	0	0	x	—	—
<i>Kaloula conjuncta negrosensis</i>	—	—	—	x (8)	—	—
<i>Lepidodactylus brevipes</i>	2	2	0	—	—	—
<i>Mabuya multicarinata</i>	0	0	0	x	—	—
<i>Mabuya multifasciata</i>	0	0	0	x	—	—
<i>Lygosoma (Leiopisma) a. auriculatum</i>	8	6	0	x	—	x
<i>Lygosoma (Sphenomorphus) a. arborens</i>	12	2	0	x (17)	x	—
<i>Lygosoma (Sphenomorphus) steerii</i>	27	5	1	x (10)	—	—
<i>Brachymeles gracilis taylori</i>	2	2	0	x	x	—
<i>Brachymeles schadenbergi talinis</i>	0	0	0	x	—	—
<i>Calamaria gervaisi iridescens</i>	3	0	0	x	—	—
<i>Cyclocorus lineatus</i>	2	0	1	x	x	—
<i>Oligodon modestum</i>	0	0	0	—	x	—
<i>Pseudorabdion menamarae</i>	0	0	0	x	—	—
<i>Pseudorabdion montanum</i>	0	0	1	—	—	—

* For Quadrat No. 1 these figures are extrapolated from those for 610 m².

** *Rana s. everetti* is omitted from this table since it has not been collected in the submontane zone on the eastern or northern slopes of the mountain, but it is known from corresponding altitudes on the southwest side.

*** Numbers given in parentheses indicate those species for which the cruising sample at given altitudes was 5 or more during the period from March 22 to May 13, 1958.

TABLE IV. Numbers of specimens obtained in sampling of forest amphibians and reptiles in the montane forest of Cuernos de Negros

Species	Quadrat No. 4 (929 m ² alt. 1425- 1450+m)	CRUISING*	
		1400-1475 m	1475-1750 m
<i>Cornufer hazelae</i>	15	x (37)	x (10)
<i>Cornufer meyeri</i>	122	x (6)	x (21)
<i>Lygosoma (Sphenomorphus) a. arborens</i>	1	x	—
<i>Lygosoma (Sphenomorphus) steerii</i>	1	x	—
<i>Calamaria gervaisi iridescens</i>	0	x	—
<i>Pseudorabdion montanum</i>	1	—	—

* Numbers given in parentheses indicate those species for which the cruising sample at given altitudes was 5 or more during the period from March 22 to May 13, 1958.

lected at altitudes above 925 m, and, as noted, 7 of these *Rana magna visayanus*, *Cornufer corrugatus*, *Lygosoma (Leiopisma) pulchellum taylori*, *Cyrtodactylus philippinus*, *Lygosoma (Sphenomorphus) jagori grande* and *Natrix n. negrosensis* have not been taken above 975 to 1025 m. Others drop out at various altitudes in the submontane and montane zones. Only 2 amphibians, *Cornufer hazelae* and *Cornufer meyeri*, are found at altitudes above 1450 m.

TABLE V. Results of population sampling of *Cornufer meyeri* and *C. hazelae* for quadrats established at different altitudes in the montane and submontane forests

	Observed	Expected
<i>Cornufer meyeri</i>		
Average of quadrats 1 and 2 (Altitude, 1100 m).....	55	90.33
Quadrat 3 (Altitude, 1275 m).....	94	90.33
Quadrat 4 (Altitude, 1425 m).....	122	90.33
<i>Cornufer hazelae</i>		
Average quadrat 1 and 2 (Altitude, 1100 m).....	17.5	14.5
Quadrat 3 (Altitude, 1275 m).....	11.0	14.5
Quadrat 4 (Altitude, 1425 m).....	15.0	14.5

The samples of 2 species of forest frogs (*Cornufer meyeri* and *Cornufer hazelae*) are sufficiently large for quadrats 1 to 4 that a Chi-square test of the hypothesis that the samples for each of these species were drawn from a uniformly distributed population within the altitudinal range of the quadrats (Table V) can be made. When the samples of *Cornufer meyeri* are compared the Chi-square value of 24.95 with 2 degrees of freedom corresponds to a probability of less than .001 that these samples are from a uniformly distributed population and supports the hypothesis of an increasing density from the lower boundary of the submontane forest to the lower boundary

and transitional dipterocarp-submontane zones (Tables II-IV) have been tentatively established.

Only 27 of the 51 forest species have been col-

of the montane forest and possibly to the summit of the north peak. When the samples of *Cornufer hazelae* are compared, with the same number of degrees of freedom, the Chi-square value of 1.477 corresponds to a probability of about one in three that these samples were taken from a uniformly distributed population between 3500 and 4800 feet. An explanation of the increase in population density for *Cornufer meyeri* in correlation with increasing altitude in the submontane and lower montane zones may possibly be found in the decrease of actual predators. The failure of *Cornufer habelae*, the arboreal frog, to exhibit an increase in density as altitude is increased within the submontane and montane zones would seem more likely to be related to incidence of available sites in the arboreal strata.

Let us consider also what inferences are possible concerning the population densities for any given species relative to any other species and also the density of a species relative to the availability of any requisite in its environment. An examination of tables III-IV reveals that the 5 species, *Cornufer hazelae*, *Cornufer meyeri*, *Lygosoma (Leiopisma) auriculatum*, *Lygosoma (Sphenomorphus) arborens* and *Lygosoma (Sphenomorphus) steerei* which exhibit a relatively high density (5 or more per 10,000 ft² based on the quadrat sampling technique at various altitudes in the submontane and lower montane zones) were also the species (with the exception of *L. auriculatum*) which were commonly obtained by cruising techniques at corresponding altitudes. We have chosen to call these species common, for the altitudinal ranges concerned, in the sense that they are much more numerous per unit of area than are other species at the same altitudes. The other 15 species for which quadrat samples in the submontane or montane zone ranged from 0 to 3, never greater, and which were also typically less frequently represented in cruising samples are arbitrarily classified as relatively rare species throughout the altitudinal range in the submontane zone at which each species is known to occur. The reptiles occurring in the lower altitudes of the montane zone are all regarded as rare.

We recognize the limitations of the small number of quadrats. However, each quadrat, explored as outlined in the section on methods, represents from 75 to 250 man hours of effort and the results as indicated in Table VI are rather uniformly good, ranging from 50% to 60% for snakes; 62.5% to 100% for lizards and 50% to 100% for amphibians. It should also be noted at this point that the sample values for the quadrats may be assumed to be minimal values since the

TABLE VI. Comparison of quadrat and cruising samples with the total number of species in the montane, submontane and transitional dipterocarp-submontane zones

		No. of species of Amphibians	No. of species of Lizards	No. of species of Snakes
Montane Zone (1400-1750 m)	Cruising	2	2	1
	Quadrat No. 4	2	2	1
	Total known species	2	2	2
	Quadrat sample	1.00	1.00	0.50
	Total			
	Cruising sample	1.00	1.00	0.50
Submontane Zone (1080-1350 m)	Cruising	4	7	5
	Quadrat Nos. 1, 2 and 3	3	5	3
	Total known species	4	8	5
	Quadrat sample	0.75	0.625	0.60
	Total			
	Cruising sample	1.00	0.875	1.00
Transitional Dipterocarp Submontane Zone (925-1000 m)	Cruising	3	6	3
	Quadrat No. 5	2	6	3
	Total known species	4	8	5
	Quadrat sample	0.50	0.75	0.60
	Total			
	Quadrat sample	0.75	0.75	0.60

collecting methods are probably in no instance 100% efficient and since any movement of these secretive animals would be expected to be outward from the disturbed area rather than inward from the surrounding undisturbed forest.

When we consider the montane forest area alone the single quadrat produced 83% of the total species known and the cruising sample accounted for 83% of the total species. About 75 man hours of effort were spent on the montane quadrat, somewhat more in cruising. In the submontane forest area the 3 quadrats yielded 76.5% of the total species and the cruising sample 94%. In the transitional dipterocarp-submontane forest area the single quadrat yielded 61.1% and the cruising sample 77.7% of the total species. However, in the latter 2 instances, the cruising sample was supplemented by earlier collections in the area, while the quadrat samples were taken during the period of March 22 to May 13, 1958.

SUMMARY

Reported here are the results of investigations of the herpetofauna of the tropical rain-forest or the Cuernos de Negros, a 1750 m mountain in southeastern Negros Island.

The vegetation types represented in the area surveyed include montane forest above 1400 m; submontane forest between 1050 and 1350 m; transitional dipterocarp-submontane forest in some

areas from 1025 to about 925 m on the north-eastern, eastern and southeastern slopes; a few scattered patches of dipterocarp forest and some secondary growth especially along streams at lower altitudes on the same slopes and in the coastal plains; "strand" and swamp areas near the beach and some small grassland areas.

Amphibians and reptiles were sampled by cruising and quadrat techniques. The latter method was limited to the transitional dipterocarp-submontane, submontane and montane zones. Arboreal, surface and sub-surface strata were sampled.

Of the total of 67 species now recorded, 10 are non-forest forms, and 6 are so inadequately known that they are not considered in our discussion. Of the remaining 51 forest-inhabiting species, 50 occur in the dipterocarp zone. However, one of the frogs, *Cornufer hazelae* is rare below the submontane zone, being replaced by its ecological equivalent, *Cornufer guentheri*. The only species absent from the dipterocarp zone is a snake, *Pseudorabdion montanum*. Of the 50 lowland species, 19 inhabit the submontane zone, and 5 the montane zone. These 5 species are apparently tolerant of a wide range of conditions. Thus 31 species (about 3/4) of the known forest species are limited to the forest at altitudes below the submontane zone.

Only 2 frogs and 3 lizards, 25% of the species occurring in the submontane zone, may be regarded as common. Of these the 2 frogs are abundant throughout both the submontane and montane zones. The 3 lizards are abundant only at lower altitudes in the submontane zone. Two of these lizards, however, along with 2 snakes occur in the lower edge of the montane forest but all 4 are relatively rare there.

Six of the 20 species in the submontane and montane zones are arboreal; one of the frogs is aquatic, and the other 13 occupy the surface, litter and loose soil strata.

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GROWTH, LOCAL MOVEMENTS AND HIBERNATION OF THE MANITOBA TOAD, *BUFO HEMIOPHRYS*¹

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INTRODUCTION

The objectives of this study were to investigate the ecology of the Manitoba Toad. This report deals with growth, local movements, and hibernation. The research was conducted on the Waubun Prairie Research Area, a 640 acre tract containing approximately 250 acres of virgin prairie. It is located in northwestern Minnesota in Mahnomen Co., Sec. 27, 28, and 33, T. 143 N., R. 42 W., of the 5th Principal Meridian. This area was acquired by the Minnesota Department of Conservation in 1954 and has been set aside specifically for basic research.

The Waubun Prairie lies within a gently rolling recessional moraine about 15 miles in width. This moraine is bounded on the east by the high continuous Big Stone Moraine and on the west by the lower discontinuous Erskine Moraine. The recessional beach lines of glacial Lake Agassiz begin on the western slopes of the Erskine Moraine.

The soils on the upland are predominantly Hamerly and Vallers loams (calcium carbonate solonchak) developed on a poorly-drained undulating till plain. A loam to silt-loam texture with weak, fine, granular structure is present in most places to a depth of 14-18 in. This grades into a clay loam with massive structure at a depth of about 36 in. (Rust 1958).

The climate of the region is continental in character and is marked by occasional drought periods and seasonal extremes in temperature (U.S. Departments of Commerce 1954, and Agriculture 1934, 1941). The mean annual temperature as recorded at Mahnomen, approximately 12 miles north of the study area, is 40°F and the seasonal means are: Winter, 8°F; spring, 40°F; summer 67°F; and fall, 43°F. Temperatures above 100°F usually occur each summer and winter lows of -20 to -30°F are common. The growing season is approximately 111 days between the average dates of May 29 and September 17.

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Annual precipitation averages 20.6 inches of which about 75% is received during the growing season from May through September. Periods of drought from one to 4 weeks in duration often occur during this period. Winter snowfall averages 36 inches annually.

The vegetational cover in this portion of Minnesota was originally tall grass prairie with extensive marshes and some thickets of aspen *Populus tremuloides*, and willows *Salix* spp. (Ewing 1924, Upham 1884). To the east a narrow belt of deciduous forests, mainly sugar maple *Acer saccharum*, basswood *Tilia americana*, aspen, and oaks *Quercus* spp., largely replaced the prairie at the margin of the Big Stone Moraine. Only a few miles farther east coniferous forests intermingled with the deciduous trees. To the west, the tall grass prairies originally extended over the Erskine Moraine and across the Red River Valley. Some deciduous forest islands occurred on the moraine.

Isolated tracts of native prairie remain although most of the land is farmed. Waubun Prairie is such a tract that lies in an ecotone between the forests to the east and prairies to the west.

Originally, prairie conditions were probably maintained in the area by frequent fires set by lightning and/or Indians (Buell and Facey 1960, Sauer 1944, Stewart 1951). In recent years, with more effective fire control, a rapid spread of aspen and willow has occurred. Currently, agricultural drainage and roadside ditching have lowered the water table allowing extensive cultivation, although numerous marshes and potholes persist.

The vegetation of the uplands of the Waubun Prairie is characterized by big bluestem *Andropogon gerardi*, little bluestem *A. scoparius*, Indian grass *Sorghastrum nutans*, and needlegrass *Stipa spartea*. In the marshes, cattail *Typha latifolia*, reed *Phragmites communis*, bullrush *Scirpus acutus*, and sedges *Carex* spp. are commonly found. The major woody plants are aspen and willows.

Bufo hemiophrys, the only species of toad on the Waubun Prairie, was abundant and this presented a highly favorable situation for a study of its ecology.

GROWTH

Methods

An accurate method of describing size is basic to any study of growth in an animal. Body lengths were measured with calipers from snout to the posterior end of the urostyle. We considered the usual snout-vent measurement to be too variable because of the flexible nature of the soft tissue surrounding the vent. The sharp angle formed by the urostyle when the toad is in a normal resting position is relatively firm and definite. Numerous repeated measurements of single individuals indicated that this measurement is accurate to $\pm .5$ mm. This measurement is slightly less than the snout-vent length.

Recognition of individual animals was accomplished by toe-clipping with the toes of the fore feet indicating units; the left hind foot, tens; and the right hind foot, hundreds. Many numbers used were not consecutive. Clipped toes regenerated over periods of several months. Regenerated toes appeared shorter, lighter in color, and often had a peculiar pointed and hooked shape. We believe that we could recognize all marked toads for a period of about 12 months following toe-clipping. Many could be identified for longer periods.

We toe-clipped 37 toads during 1957, 134 in 1958, and 178 in 1959 for a total of 349 adult and sub-adult toads. Newly metamorphosed animals had a high mortality rate during the first few weeks of life. We considered it inadvisable to mark this age group since the percentage of returns would be impractically low. Growth data for these were obtained by measuring groups of toads collected periodically during the summer.

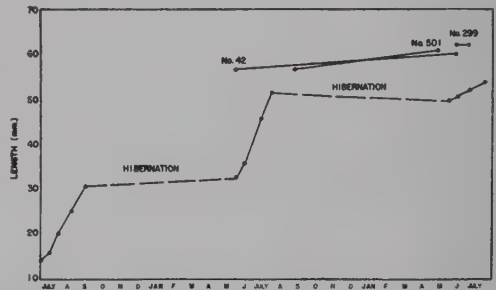
By far the most successful method of retrieving marked animals was by daytime hand collecting along the margins of the ponds. During 1957 and 1958 screen wire traps were located on the uplands and adjacent to different types of ponds. The traps were 3 feet square divided diagonally into 4 sections with a funnel entrance into each section and with asphalt roofing paper lead fences 12 in. high and 27 ft long extending from each corner. Night collecting with flashlights had no advantage over day collecting except during the calling period in spring.

Results

Two important aspects of growth studies are the determination of the period required for the animal to reach maturity and the rates of growth at various times during this period. We were not able to investigate in detail the egg and tadpole stages of development due to our inability

to be on the area during the proper season. Our growth studies concern the period from metamorphosis to maturity.

Continuous field observations in June and July revealed the first newly metamorphosed young on June 29, 1958, on July 5, 1959, and on July 4, 1960. These toads ranged in size from 9 to 15 mm. Growth from the time of metamorphosis to hibernation in the fall is shown on the left portion of Figure 1. These data were obtained from groups of 13, 18, 21, 35, and 8 individuals. There is a wide range in length of toads comprising these samples (e.g. 11 mm to 27.5 mm in the July 30, 1959 collection). This suggests that, although individual growth rates vary, metamorphosis occurs over a period of several weeks. This is supported by the fact that males call over a period of nearly 2 months which probably indicates an extended egg-laying period.



1 representing the actual average size of 2nd-year toads at the time of hibernating. However, the fact that we failed to locate marked toads of this age class after August 1 suggests that either they enter hibernation early or grow but little during August. We have evidence, discussed later, that many of the larger toads enter dormancy in late August or early September.

The right hand segment of the curve in Fig. 1 represents the growth of toads we believe to be in their 3rd growing season. The points are each based on from 4 to 7 records of marked individuals.

The growth rate of toads approaching maximum size, whose age we were not able to determine, apparently decreases markedly as indicated by the records for toads No. 42, No. 299, and No. 501 (Fig. 1).

The slopes of the curves representing the growing periods in a toad's development reveal a high absolute growth rate in the first and 2nd season and a lower rate in subsequent seasons. The growth rate of toads larger than 25 mm expressed as % increment in length per day is presented in Figure 2. This curve, based on growth of marked individuals, shows a steadily declining rate of increment as the toads mature.

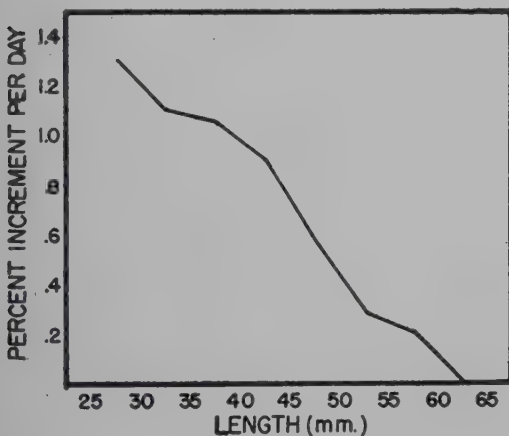


FIG. 2. Percent increment in length per day of *Bufo hemiophrys*.

We did not observe any differences in growth rates between the sexes. The largest individuals measured during the study were females (largest male, 60 mm; female, 68 mm).

LOCAL MOVEMENTS

Methods

Random retrieving of marked individuals has been the usual method in the past of securing data

concerning local movements of animals (Fitch 1958, Pyburn 1958). We used this method during 1957 and 1958 but secured few data. In 1959 we turned to radioactive tagging as a method of following these toads. Certain toe-clipped individuals were marked with radioactive tags and located periodically with a scintillation counter.

Ta¹⁸² was chosen as the tagging material for 3 reasons: (1) it discharged gamma rays at a high energy level (1.2 MEV) for penetration of soil and water, (2) its comparatively short half life of 117 days, although not ideally suited to such an extended study, provided a safety factor in case a tag was lost, and (3) it was available in wire form.

A charge of 100 μ c (actual charge was 100 μ c $\pm$ 50% according to Oak Ridge National Laboratory) was chosen on the basis of findings by Karlstrom (1957), Griffin (1952), Pendleton (1956), and Godfrey (1954, 1955) as being sufficiently strong for field detection and yet below the strength which might injure the animals over periods of several months. Pieces of Ta¹⁸² wire 1 mm in diameter and 5 mm long were inserted beneath the skin of the anterior dorsal region. The tags were not encapsulated or treated in any manner before implantation. This was done upon recommendation of James Marvin, Radiology Department, and Ralph Wollan, Health Physicist, both of the University of Minnesota Hospital staff. A large hypodermic syringe with a stylet attached to the plunger was used for inserting the pellet. Long forceps served to insert the Ta¹⁸² pellet into the tip of the needle before injection.

We found that this technique had little effect on local movements and hibernation. This evidence will be presented later. Twelve measurements of tantalum-marked toads over periods of several weeks show that growth was identical to that of unmarked toads. The technique did cause detrimental physical effects in a few cases. We did not attempt to maintain sterile conditions during injection. One toad (No. 504) was noted as having a swelling at the location of the pellet but this animal was found to be normal 3 days later. Three tags were found on the ground with no evidence of the death of the toads bearing them. In one case (No. 328) the tag was known to have slipped out of the incision the day after marking. The other 2 tags may have caused local infections which later burst releasing the pellets although the toads may have been eaten by predators and the tags cast in droppings.

Toad 505 was tagged on August 31, 1959 and was found burrowing into its hibernation site on September 5. It remained at a depth of only

7 inches until November 3 when we partially exposed it momentarily and found it to be alive. This toad, unlike the other hibernating animals, did not burrow deeper during the winter and was found dead in this location on June 23, 1960. The fact that this abnormal behavior occurred within a period of only a few weeks of being tagged strongly suggests that this was due to infection or other physical injury caused by the tagging and not radioactivity.

Field tests showed that tagged toads could be detected on the surface at about 20 ft while a buried animal carrying a 4 month old charge was located 22 in. deep in silty clay loam soil. Animals marked with nearly fresh charges could be detected in 16 in. of water at a distance of 4-5 ft. The identity of a toad could not be determined from its tag; however, the toe-clipping system provided positive identification of each individual. Animals in the field were located with reference to plainly visible surveyed grid points at 300 ft intervals and positions were recorded on large scale maps.

Weather data were obtained from the records of the U.S. Weather Bureau Station at Mahanomen, 12 miles north of the area.

Results

One objective of the study of local movements was to determine the extent of use by the toads of the various habitats present. During 1957 and 1958 six traps were operated for varying periods sampling populations in different habitats (Table I). Populations varied markedly with at least small numbers visiting the trap on the highest point farthest (200 ft) from water (Trap 6). The largest populations were indicated by captures in Traps 1 and 2, adjacent to a 15-acre pond. This pond, with relatively stable water level, had gradually emerging shores with some mud flats, floating mats of sago pondweed *Potamogeton pectinatis* and filamentous algae in the shallow water, and was surrounded by a narrow belt of cattail and bullrush. The 3 remaining traps were located near ponds lacking open mud flats and had shallow marginal zones with dense stands of sedges. The small catch in these traps and our field observations indicate that few toads occupied this type of habitat.

The annual period of activity for these toads begins with their emerging from hibernation and congregating in the pond margins in May. This event is so completely dependent on weather conditions that this date varies greatly. Our earliest record of active toads in 1957 was May 22, in 1958 May 31, in 1959 May 5, and in 1960 May

TABLE I. Trap catches of the Manitoba toad, Waubesa Prairie Research Area, Minnesota, 1957-1958

Trap number	Approximate distance from water (ft)	Days in operation	Number of toads captured	Toads per day
1.....	25	95	42	.442
2.....	25	82	28	.341
3.....	25	124	15	.121
4.....	25	76	8	.105
5.....	50	90	7	.078
6.....	200	120	17	.141

11. These dates probably vary from actual emergence dates since we were not able to observe continuously during May. The breeding cycle was not observed in detail but calling extended into early July. After the breeding period adults were encountered most frequently along the pond margins throughout their season of activity. During the period when we followed the tagged toads no difference in the activities of the sexes was observed.

Almost immediately after metamorphosing many of the tiny young dispersed onto the uplands as indicated by numerous catches in Trap No. 6, 200 ft from the nearest water, on July 11 and days following in 1957. However, large numbers remained along the open mud flats near where the eggs were laid and some young in all stages of development were found there throughout the summer.

The cessation of activity in fall is gradual, the animals disappearing over several weeks from late August to mid-October. As discussed later, evidence points to the adults hibernating earlier than the young of the year.

Detailed study of the local movements was carried on with the aid of radioactive tagging. Nineteen animals were marked with Ta^{182} and were followed through their day-to-day activities for periods ranging from 2 to 90 days. Some individuals were "lost" for periods varying from one to 89 days and some were never relocated. The exact locations of individuals from one day to the next were determined in 276 instances (Table II).

On 17 occasions we recorded the location of individual toads several times (2-6) during a 24-hour period. We found no tendency toward greater movement at any part of the 24-hour period nor any tendency to occupy a particular habitat at any specific time of day.

Usually the extent of daily movements was not great but at times toads traveled considerable distances in short periods (Tables II and III).

TABLE II. Daily movements of toads, Waubun Prairie Research Area, Minnesota, 1959

Distance (ft)	Frequency
0.....	48
1- 10.....	30
11- 30.....	67
31- 60.....	49
61-100.....	39
101-150.....	21
151-200.....	10
201-300.....	7
301-400.....	4
750.....	1

TABLE III. Long movements of toads over more than 24 hours, Waubun Prairie Research Area, Minnesota, 1959. (See text for explanation)

Distance (ft)	Days "Lost"
120.....	3
160.....	89
200.....	11
240.....	46
250.....	1
325.....	2
375.....	8
400.....	2
400.....	35
400.....	72
650.....	1
875.....	44
880.....	1
920.....	7
1080.....	4
1120.....	8

About 84% of the daily movements were 100 ft or less while only 4% were more than 200 ft.

The average distance between the most widely separated points recorded for the 18 individuals during the summer was 565 feet (range: 50-1280). This suggests what might be called a home range.

It was found that there was a strong tendency for an individual to remain for a number of days within a limited area and then suddenly to move to some other area for a period. Figure 3 shows an example of this type of movement. Other animals were very sedentary (Figure 4). These data indicate that the toads live a large part of their active lives along the margins of ponds. However, some of the longer moves of tagged individuals from pond to pond led over as much as 450 ft of dry upland.

Only 2 individuals showed any tendency toward homing. Toad 225 was originally taken on the northwest shore of the pond on June 1, 1959 (Figure 5) and placed in the control pen 300 ft to the north. After 20 days it disappeared from the control pen and was located 4 days later 1280

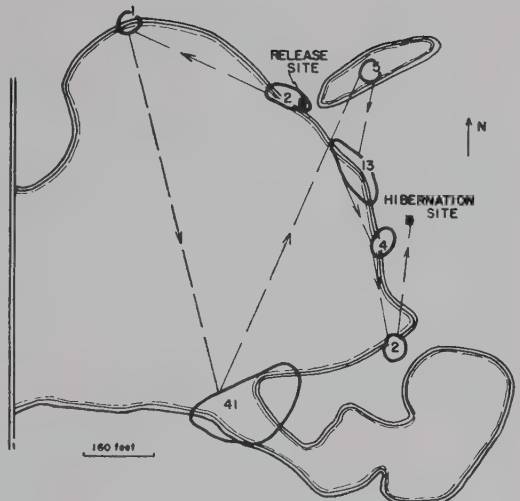


FIG. 3. Movements of toad No. 283, June 17 to August 24, 1959. Encircled numerals indicate number of days toad spent in the indicated locality. Broken lines show direction of movement but do not necessarily indicate route.

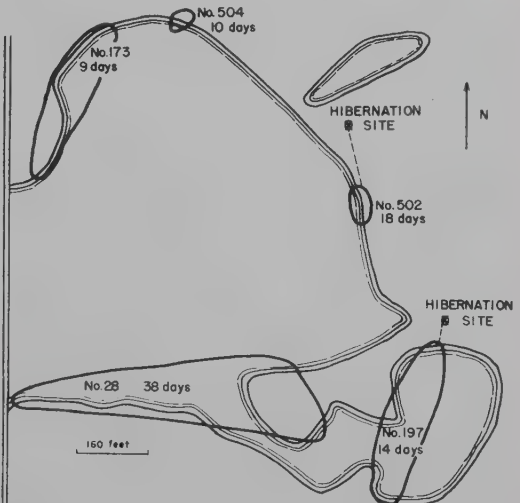


FIG. 4. Ranges of 5 Manitoba toads during the periods of traced movements, Summer, 1959. Records for each toad are from day of tagging to day of last observation.

ft to the southeast across the pond. It was immediately returned to the control pen from which it again escaped 2 days later and after 7 days it was found 1120 ft to the southeast only 160 ft from its former location. It remained in this area for 11 days when it moved 650 ft north. The toad stayed in this area for 12 days until "lost" on

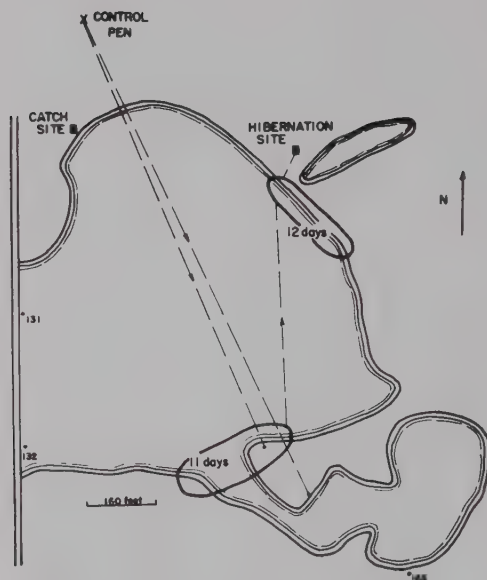


FIG. 5. Movements of toad No. 225, June 1 to July 26, 1959. Encircled numerals indicate number of days toad spent in the indicated localities. Broken lines show direction of movement but do not necessarily indicate route. See text.

July 26. Forty-six days later on September 10 it was located in its hibernation site on the upland 100 ft to the northeast of its last known location.

No. 284 was first taken at the southeast corner of the pond (Figure 5) near grid 166 on June 17, 1959. It was placed in the control pen nearly 1600 ft northwest of its point of capture where it remained until June 20 when it escaped. On June 24 it was found 1120 feet directly south on the south shore of the pond where it remained for 33 days. This animal in returning from the release point may have encircled the lake on the east in which case it would have gone almost directly toward its point of capture, it might have followed the rocky road fill south past grid points 131 and 132, or it could have gone directly south across the pond. In any case, it spent the summer in an area over 1000 ft closer to its point of capture than the release point (control pen), but still approximately 350 ft west by north of its capture point.

Certain tagged toads were lost. Some may have moved from the area and others may have burrowed so deeply during aestivation and/or hibernation that we could not detect their presence. Still others may have been removed by predators such as American bitterns, marsh hawks, great blue herons, raccoons, mink, badgers, or garter

snakes. The secretions from the paratoid glands are highly distasteful to many predators. We have positive evidence of predation only in the case of the plains garter snake. It has been reported that badgers will prey extensively on toads (field notes of Martin K. Nelson, State Game Warden, Ada, Minnesota).

The relations between weather conditions and the extent of toad movements were studied in an attempt to find some statistical correlation. We anticipated that the more extensive movements would take place during rainy or cool periods but the data showed no apparent relation between movement and temperature or precipitation.

Two difficulties complicated such calculations. One was that when toads moved the longer distances, several days often elapsed before they were again located and, as a result, the movement could not be assigned to any particular day. Another handicap was that reported precipitation, being recorded only every 24 hours, may have fallen during either one or both days of a 2-day period.

In spite of the essentially sedentary nature of these toads, we found only one animal that exhibited anything suggesting aestivation. Toad 249, a large adult male, remained dormant buried in the grass and surface litter back from the water's edge between June 27 and July 2 (5 days); July 15 to July 22 (7 days); and July 28 to August 5 (8 days). Late in our period of observation we realized that animals partially buried almost invariably moved immediately after being disturbed even though they were gently handled, replaced and covered carefully. For this reason, records of additional periods of dormancy may have been missed.

HIBERNATION

Methods

Our study of hibernation was a continuation of the investigation of local movements. Consequently the individual marking by toe-clipping and the Ta^{182} tagging with scintillation counter detection continued as the essential methods. Since we could not handle the toads without disturbing their activities, we were not able to identify individuals as they began hibernation. They were identified after emergence in the spring.

Soil temperatures at depths to which the toads might burrow were essential since an animal's reaction to temperature constitutes a major consideration in hibernation studies. These data were obtained from thermocouples buried near the hibernation site. Terminals were placed at 4 in. intervals to depths of 5.5 ft at a lateral distance

of about 12 in. from each hibernating toad. A $\frac{3}{4}$ in. square wooden bar 7 ft long was grooved on one side and holes were bored through from the groove at 4 in. intervals. Copper-constantan thermocouple wires were placed in the groove with the thermocouples projecting through each hole to a distance of about $\frac{1}{2}$ in. These were coated with polyester resin to protect them from corrosion or mechanical damage. The wires were brought along the groove to the surface and soldered to the 16 terminals of a rotating switch. The switch box was tied into a plastic bag and placed under a square of roofing paper to minimize moisture interference between recording periods. Temperature readings were taken with a portable potentiometer at 3 to 4 week intervals through the period of hibernation.

Small mesh wire fences 4 ft in diameter, capped with screen, were placed over all hibernation sites to insure the capture of the emerging animals.

Depth determinations of the burrowing animals were secured by drilling 3 in. holes with a bucket-type soil auger about 12 in. laterally from the animals to a depth of 6 ft. These were drilled at the time the hibernation sites were located. The probe of the scintillation counter was lowered into each hole and the intensity of radiation recorded at 2 in. intervals. Between observation periods the holes were closed with 8-12 in. grass or burlap plugs capped with sod and covered with roofing paper. Difficulties arose from the freezing of the plugs to the surrounding soil and from accumulations of snow melt-water. In future studies we plan to insert plastic tubes sealed at the bottom and with removable caps to allow free use of the scintillometer probe during winter and early spring.

Results

Entrance into hibernation

Our data indicate that most toads begin hibernation in late August and early September. All of the tagged toads whose local movements were being followed in late summer were temporarily "lost" between August 27 and September 16. The hibernation sites of 6 radioactive toads were located between September 7 and 16.

Our records on the size of toads found on the various dates suggest that the large adults tend to hibernate earlier. One individual 30.5 mm in length was found active on the surface as late as October 14, 1959.

Location of hibernation sites

Six out of 7 toads whose hibernation sites were found in the fall of 1959 burrowed in small earth

mounds 10 to 40 feet in diameter and one to 2 feet high which are scattered over the uplands. The possible origin of similar "Mima-type" mounds has been extensively discussed in the literature (Arkley and Brown 1954, Scheffer 1958). We believe that they are at least partially the result of pocket gopher activity. The mounds are covered by coarse weedy plants in contrast to the surrounding prairie flora.

To verify our suspicions that toads used these mounds extensively for hibernation, we erected 18 inch sheet metal fences around two areas 100 feet in circumference. One surrounded a mound and one surrounded an equal area of open prairie adjacent to the mound and with the same relation to the nearby pond. These were placed on April 26 just after the surface soil was free of frost and before any toads had emerged. A screen trap 3 feet square with a conical entrance was placed on the side of each pen nearest the pond to trap all emerging toads as they moved toward the water.

No toads were found at any time in the open prairie pen while 225 were taken from the pen surrounding the mound. The extent to which the toads utilized these earth mounds may prove significant not only in its connection with the ecology of the animal but also as it may pertain to the possible origin of the mounds.

Winter activity

Our data revealed that most of the toads moved vertically during the winter. Five of 6 individuals studied survived the winter and emerged in good physical condition. Figures 6-9 show what appears to be a relation between soil temperatures and burrowing movements. All 5 toads burrowed vertically to depths of 18 to 26 inches by mid-October. Number 502 continued to burrow deeper throughout November and December to a depth of 32 inches where it remained with little movement until spring emergence. The other 4 did not move until January or February when the soil temperatures began dropping rapidly. At this time all appeared to react more or less extensively to the reduced temperature by burrowing deeper. The maximum measured depth of hibernation was 46 inches.

Figures 6 and 7 suggest that these animals moved upward within the zone of frozen soil. This probably was not possible for 3 reasons. First, the chemical contents of the soil water probably would depress the freezing point of the soil; second, the temperature determinations were subject to some slight experimental error;

and third, the determinations of the position of the toads were only accurate within 2 inches.

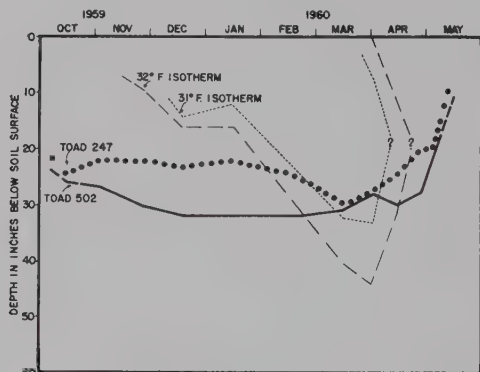


FIG. 6. Relations between depths of wintering toads 247 and 502 (sites were 8 ft apart) and positions of 31°F and 32°F isotherms in the soil.

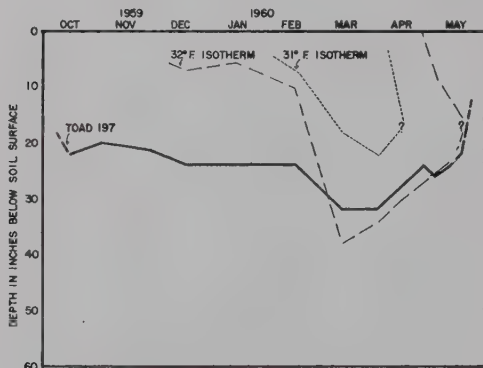


FIG. 7. Relations between depth of wintering toad 197 and positions of 31°F and 32°F isotherms in the soil.

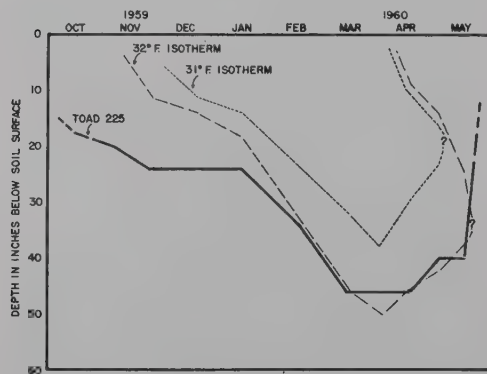


FIG. 8. Relations between depth of wintering toad 225 and positions of 31°F and 32°F isotherms in the soil.

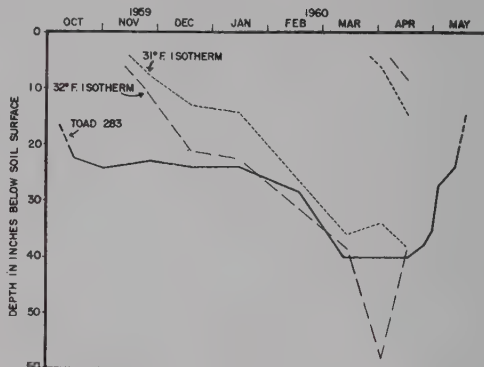


FIG. 9. Relations between depth of wintering toad 283 and positions of 31°F and 32°F isotherms in the soil.

It is pertinent to note that the frost in the soil thawed both from above and below and, with the last of the frost disappearing at between 20 and 36 inches, the animals would suddenly find themselves free to emerge rather rapidly from these points well below the surface.

Soil factors

In addition to temperature, certain soil characteristics might influence depth of burrowing. An analysis of the soil profiles at the hibernation sites of the 6 toads was made by F. M. Scille, Field Staff Specialist, U. S. Soil Conservation Service.

The characters of color, texture, structure, consistency and effervescence were examined at approximately 6 inch intervals to depths of 5 feet with a bucket-type soil auger. Minor changes were noted in some of these characters at the points of maximum penetration by the toads but no changes common to all sites were detected. We concluded that the depth of penetration was not influenced by any of the soil characters examined.

Toad 505 dug 7 inches from the surface through soil with massive structure and remained at this depth. The structure from 7 to 17 inches at this site was very weak, very fine, subangular blocky. Other toads dug in soil of this structure. No explanation is postulated for the hibernation behavior of this individual other than the possibility that it may have been injured during injection of the radioactive tag.

Emergence from hibernation

We secured our most pertinent data on spring emergence from the metal pens. Of the 225 toads secured (Figure 10) the earliest were found

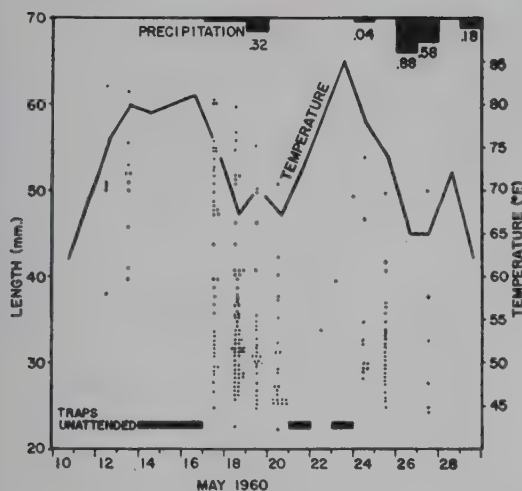


FIG. 10. Relations between precipitation, maximum air temperatures and spring emergence of toads of different body lengths. Dots represent 225 individuals which emerged from one "Mima-type" mound 33 ft in diameter.

on May 12, 1960, the same day that the first calling was heard. The last were taken from the pen on May 27.

The earliest toads to emerge were in a ratio of 4 adults to one young (Fig. 10); the May 17 take, which represents those emerging from May 14 to 17, was made up of young and adults in about equal numbers; after May 17 the daily takes were all predominately young with an average ratio of 9 young to one adult.

Fig. 10 also shows that the first toads appeared during the first warm period following the disappearance of soil frost (Figs. 6-9). The main body of the population emerged during the first rainy period 5 days later. The 2nd peak occurred during the next rainy period, which began on May 24.

SUMMARY

The growth, local movements and hibernation of the Manitoba Toad (*Bufo hemiophrys*) were studied on a virgin prairie in northwestern Minnesota. Growth data were derived from averages of field collections for newly metamorphosed animals and from toe clipped individuals of larger size. Toads were found to be of adult size on emergence from their 2nd period of hibernation at about 23 months of age. Growth was rapid the first season, markedly less the 2nd, and extremely slow thereafter.

Local movements were studied mainly by using scintillation counters to follow toads marked with radioactive Ta^{182} . This species was found

to live almost exclusively in or near the margins of prairie ponds. There was a strong tendency for an individual to remain for a number of days within a limited area and then suddenly to move to another area. About 84% of the 276 daily movements recorded were 100 feet or less while only 4% were more than 200 feet. One animal aestivated for periods of 5, 7, and 8 days.

All toads followed hibernated on the upland 75 to 115 feet from the pond margins. Six of 7 tagged toads burrowed into small "Mima-type" mounds. A fence 100 feet long surrounding a mound trapped 225 emerging toads while a similar fence on the adjacent prairie trapped none. Some vertical movement of the hibernating toads was recorded throughout the winter. One individual avoided the descending 32° F zone by burrowing to a depth of 46 inches while others survived prolonged periods of subfreezing temperatures. In spring the zone of frozen soil thawed simultaneously from above and below, finally disappearing at from 20 to 36 inches below the surface. The toads thus were able to move upward slowly following the lower frost line until its disappearance suddenly released them for rapid emergence.

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FOOD SELECTION AMONG FISHES INVADING A HIGH SUBTROPICAL SALT MARSH: FROM ONSET OF FLOODING THROUGH THE PROGRESS OF A MOSQUITO BROOD¹

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INTRODUCTION

Food relationships of fishes and invertebrates on subtropical salt marshes and in mangrove swamps of North America are virtually unknown, although these are nurseries for immigrant young of certain food and sport fishes, and produce some of the world's densest mosquito outbreaks. Some of the fishes occur also in estuaries, where food habits are poorly known (Darnell 1958) and the habits of small species, such as cyprinodontiform fishes, have been slighted. The literature on control of mosquitoes by fishes (*cf.* Gerberich 1946, Krumholz 1948) mostly concerns predation on fresh-water anophelines by the mosquitofish, *Gambusia affinis*. With a few exceptions (*e.g.* Hess and Tarzwell 1942), these investigations were too casual or circumscribed for a perspective on food coaction. No articulated study of fish predation as it pertains to salt-marsh mosquitoes in subtropical regions of the United States has been made, even though *Aedes* mosquitos have become the chief objects of control measures since the malaria problem was resolved.

The present study was contrived to distinguish between larvivorous (mosquito-eating) and non-larvivorous fishes frequenting salt marshes and adjacent zones of the subtropical halosere in Florida, and to discriminate among larvivores as to differential consumption of successive mosquito stages and of other organisms. It was planned also to identify the categories of food organisms commonly available to fishes on a high marsh and to assess the relative importance of each.

The rationale of the study exploits an attribute

of the habitat exaggerated by a sudden change in the environment. The habitat is usually flooded only by heavy rainfall or autumn tides. A severe drought excluded fishes from the area until this food study began concurrently with an abrupt flooding by combined rainfall and high tides. The food organisms consumed by the assemblage of fishes invading the marsh were compared each day among fish species. These daily interspecies comparisons paralleled the hatching, increase to peak density, and depletion of the chief food variable, the salt-marsh mosquito, *Aedes taeniorhynchus*, and continued after the exodus of the adult mosquitoes. A telescoped seasonal food cycle with sharp onset was simulated. Such conditions prevail in the wetlands along the brackish lagoon known as Indian River, where the study was made, but were accentuated by the unusually complete change from drought to flood, which synchronized the food cycle and thus sharpened contrasts in food availability which are usual in this environment.

In lieu of the forage ratio method of assessing preference with respect to availability (*cf.* Hess and Tarzwell 1942), the composition of food organisms in the guts of one fish species was contrasted with that in the guts of the others, and compared with the collective gut contents of all fish sampled. The validity of the forage method depends on the accuracy of the habitat food analysis. In many habitats, this gives inadequate estimates of food availability (*cf.* summary of criticisms by Hynes 1950). The muddiness and heterogeneity of the gross habitat and the extreme vagility of the fishes precluded an effective habitat food analysis here.

METHODS

During the drought of 1956 in Florida, the progress of desiccation on the marsh and its

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effects on the biota were noted casually up to August 1. Observations were then stepped up in anticipation of the autumn inundation of the Indian River lowlands, the causal timetable of which has been discussed (Harrington 1958). A rain gauge and tide gauges were in operation on the marsh prior to August 1. The rain gauge and one tide gauge (Fig. 2, TG₃) were near the center

of the marsh; another tide gauge (TG₄) was at the marsh shore of Indian River to the north. Tide gauge readings were referred to mean sea level from a bench mark. Water temperatures were taken before and during the interval of fish collecting, which began with seining the morning after the marsh was flooded. Specific gravities measured concurrently were corrected to 15°C.

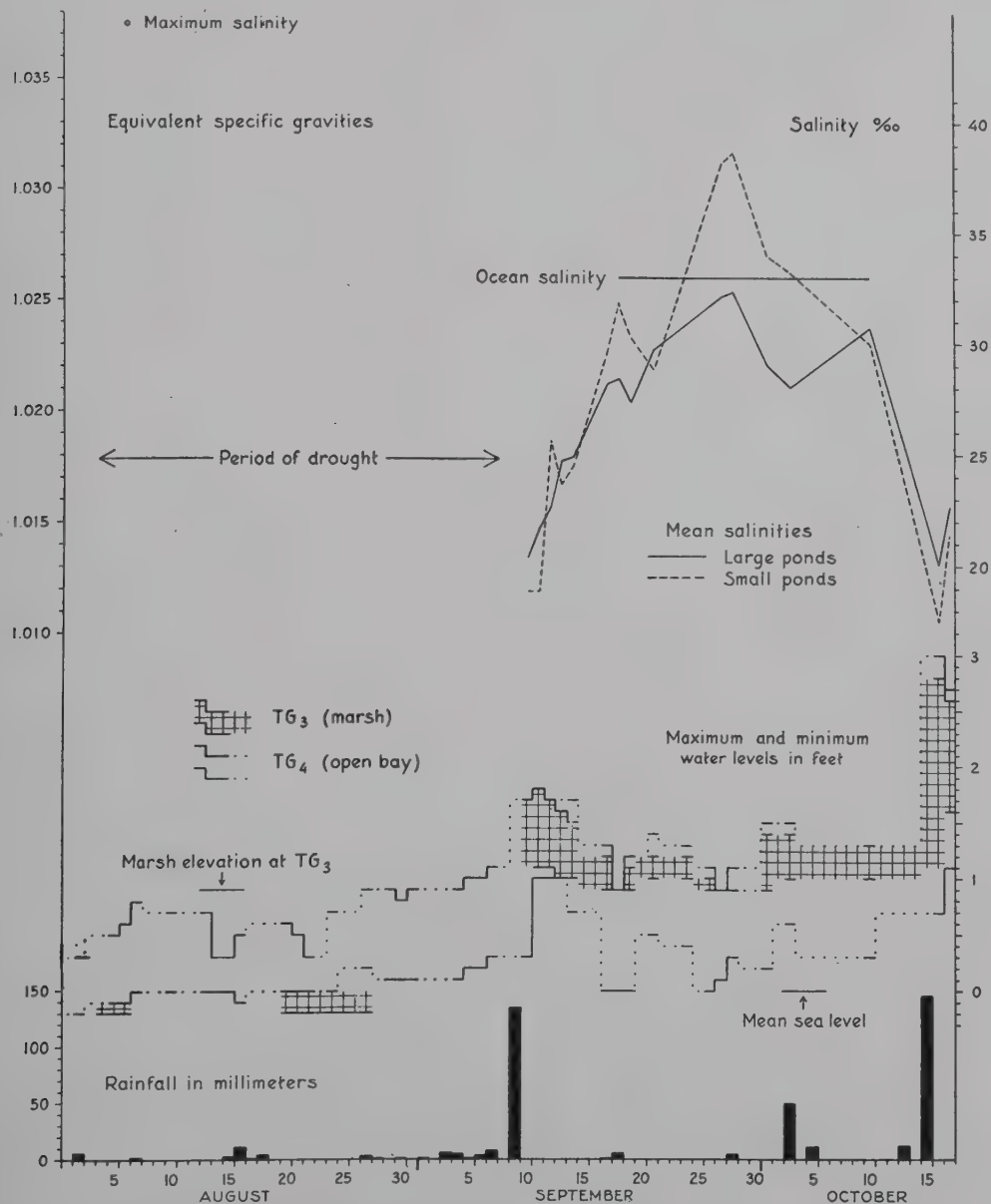


FIG. 1. Schedule of physical changes (rainfall, water level, and salinity) on the marsh the last 39 days of drought and the first 39 days of flood.

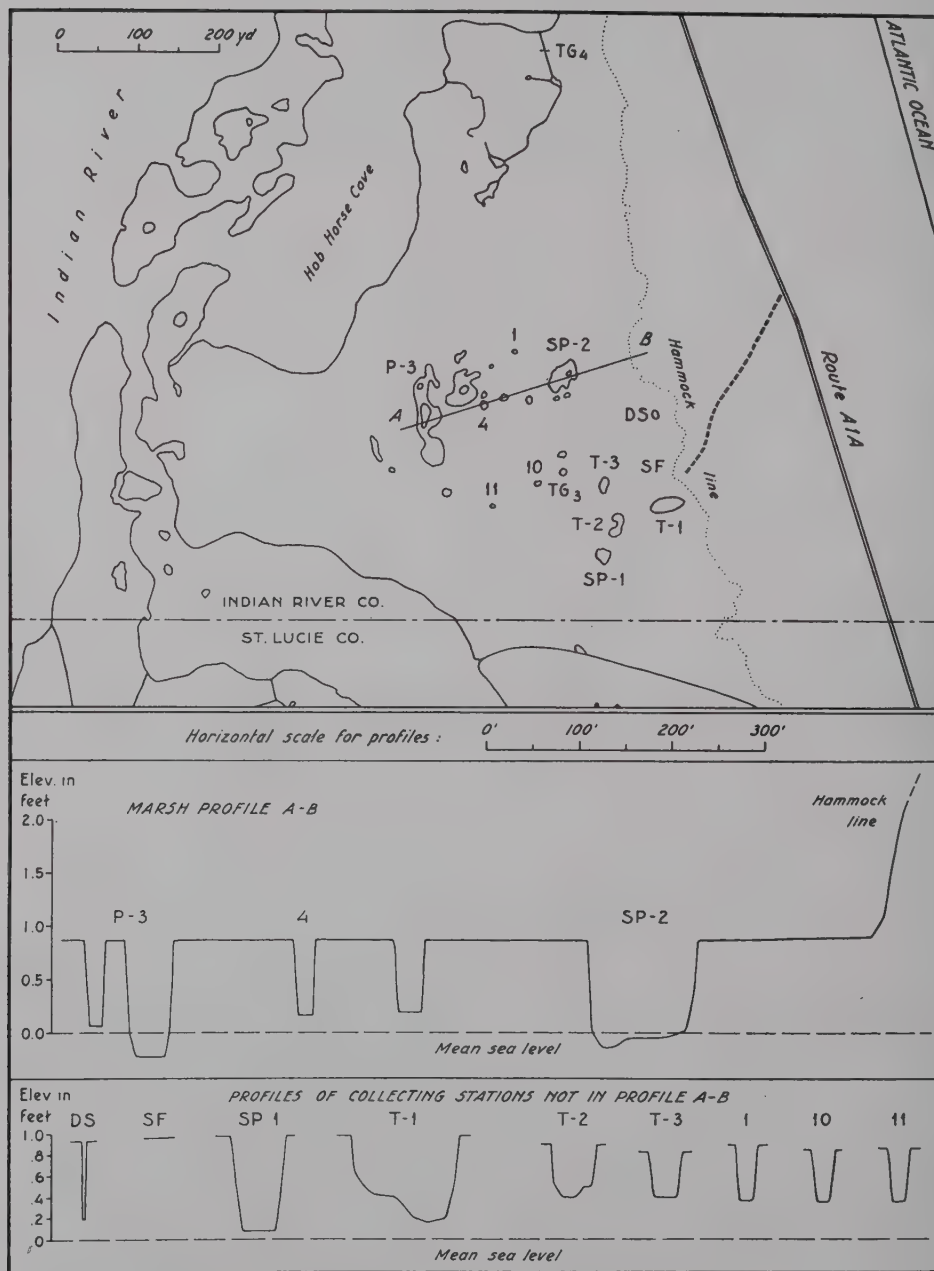


FIG. 2. Above: map of the salt marsh with positions of instrument and collecting sites. Below: marsh profiles showing elevations.

The corresponding salinities were obtained from a table (Zerbe and Taylor 1953), except for a few extreme hydrometer readings converted by graphic extrapolation. Figure 1 records rainfall, water levels, and salinities. Figure 2 defines the horizontal positions of instrument and collecting sites and their elevations, as determined by levels from the bench mark.

To minimize the influence of collecting on fish movement and feeding, unbaited slit-traps were relied on chiefly. These were set out usually in the afternoon, and emptied within 24 hours. Seining was confined perforce to the few larger ponds (Fig. 2), and employed to take species less prone to enter traps; rotenone could be used only 4 times in such a manner spatially and temporally as not to vitiate food analyses based on subsequent collecting. The collecting sites are labelled in Fig. 2, and will be mentioned in the description of the marsh; the fishes collected are considered below.

The fish were fixed in 10% formalin, washed in water, and stored in 70% ethyl alcohol. The contents of the whole alimentary tract were analyzed. This was required (1) by the morphological diversity among tracts of different fishes, *e.g.* varying from the stomachless cyprinodontid tract, through the more differentiated tarpon tract, to the specialized mullet tract, (2) by the fact that fish were entering traps at different times, and (3) because, although rate of food passage through the gut has been little studied, it may be expected to vary with fish species, fish size, and with temperature (Barrington 1957, Sokalov and Chvaliova 1936, Hunt 1953, Hathaway 1927). The objective was to determine the relative amounts of the food components wherever in the gut they chanced to be at time of fixation.

After the items in a single tract were identified, the percentage contributed by each to the total contents taken as 100% was estimated on a grid. The total contents were then measured volumetrically with a graduated centrifuge tube, and the estimated percentages converted to milliliter parts of the measured total volume (*cf.* Harrington and Harrington 1960). The grid method was extended to find the proportions of plant constituents in mullet guts, which often contained masses of intermixed, minute items. The total plant bulk was first estimated against the grid in the routine manner, then 5 samples were withdrawn and examined under higher power ($\times 430$) with a Whipple disk. The proportion of 100 squares occupied by each item was determined. These counts were averaged for the 5 samples, and the resulting percentages used to subdivide the esti-

mated total plant bulk. Table III will show to what degrees of refinement identification and measurement were carried.

DESCRIPTION OF THE SALT MARSH

The Indian River shore line of the marsh is bordered by alternating clumps of black and red mangroves (*Avicennia nitida* Jacquin and *Rhizophora mangle* L.), the latter predominating except along the margin of the shallow, saline embayment transected by the county line (Fig. 2). Along the eastern (upland) edge of the marsh runs a black mangrove slough 100 yards wide. It is encroached up to the east by a narrow band of red mangroves straddling the hammock line at the upland boundary of the marsh. The red mangrove band exceeds 50 feet in width only along the northernmost 250 yards of the hammock line, where it progressively replaces the black mangroves. Within these confines, the marsh is an expansive "parkland" of saltwort (*Batis maritima* L.) and glasswort (*Salicornia perennis* Mill.) interspersed with clumps of black mangrove. The aggregate areas of *Batis-Salicornia* and of black mangrove are roughly coequal. Black mangroves border all but the semipermanent pond (Fig. 2, SP-1) in the southeastern corner of the marsh, which is surrounded by white mangroves (*Laguncularia racemosa* Gaertn.). The soil-water salinity exceeds the tolerance of red mangroves except along the shore line, washed by Indian River, and along the hammock line, where there is ground-water seepage (*cf.* Davis 1940). The concentration of red mangroves toward the northern end of the hammock line reflects the northward flow of seepage and runoff water from the higher ground of the hammock. The marsh has a substrate of sand overlain by a thick layer of peat. Sand comes to the surface only in a salt flat extending northwesterly from the county line along the east side of Semipermanent Pond 1 (SP-1) toward Temporary Pond 2 (T-2) and in a small flat near the entrance road (Fig. 2, double dotted line). East of the sand flats and near the hammock line there are disjunct areas of sea-ox-eye (*Borrchia frutescens* (L.) D. C.) and buttonwood (*Conocarpus erecta* L.), patches of which disrupt the red mangrove band as far as just north of the road entrance. The central expanse of the marsh is otherwise as described except for the ponds, provisionally designated as permanent, semipermanent, and temporary, and as potholes, of which those used as collecting sites are labelled in Fig. 2. These depressions were the only places where collections could be made, although fishes moved freely through the stiff, dense cover, mostly

of *Batis* and of black mangrove pneumatophores, piercing the expanse of shallow water eventually covering the marsh. The arena in which the fish dispersed took in the entire halosere, from the river shore up into the *Conocarpus* transitional associates. Most of it is above usual high tide level, and dominated by the scrub mangrove facies (cf. Davis 1940), with irregular deviations from the formal zonation of the halosere into distinct vegetation communities.

SCHEDULE OF PHYSICAL AND BIOTIC CHANGES ON THE MARSH

During the long drought, preparations were made to take advantage of a fortuitous abrupt flooding, which occurred on September 9. Fig. 1, the timetable and common referent of this study, records water conditions the last 39 days of drought and the first 39 days of flood (August 1 through October 17). Before the flood, all but 3 ponds dried up. The marsh was devoid of fish except for some young *Cyprinodon v. variegatus* surviving avian predation in one pond, in a shallow residuum of water a few feet wide. This water exceeded mean ocean salinity (Fig. 1, upper left), and rose to 43° C, which is above the lethal limit of fishes tested experimentally (Brett 1956). Not all of these fish died, and some of their congeners in western North America have been found at water temperatures of 40° C (Miller 1948) and 48.9° C (Jordan and Richardson 1907), the latter being the highest recorded temperature at which fishes have been taken (Miller 1948). However, species of *Cyprinodon* tend to avoid temperatures above 36-37° C (Barlow 1958a). In the scrub mangrove facies, soil-solution salinities average about 84 ‰ and surface-water salinities about 46 ‰ (Davis 1940). The latter is near the maximum recorded in Fig. 1. The maximum salinity tolerance of cyprinodontiform fishes, including *Cyprinodon variegatus* and congeners, is roughly twice this, or 80-90 ‰ (Barlow 1958b). Another consequence of the drought or, more precisely, of the virtual postponement of rainfall to the onset of autumn tidal flooding, was the unusually dense accumulation of salt-marsh mosquito eggs, in places exceeding 10,000 per square foot, as determined by immersing dry marsh sods in pans of water and counting the larvae hatching.

The ranges between high and low water on the marsh are crosshatched (TG₃) in Fig. 1 to contrast with the tidal ranges at the Indian River shore, which are unhatched (TG₄). The tide gauge on the marsh (TG₃) was set in the bottom of an excavated pit 0.2 foot below mean sea

level, where the marsh ground level is 0.9 foot above mean sea level. Before the flood, the ground-water level fluctuated between mean sea level and the bottom of the pit (Fig. 1). High tides did not exceed marsh ground level until a few days before the deluge of September 9, and not enough then to encroach on the marsh. Sporadic light rainfall toward the end of the drought hatched a minute proportion of the bumper crop of mosquito eggs on the marsh, but all except those that hatched within a few days before September 9 perished from desiccation. The survival of a few from scattered antediluvial broods is reflected in Figure 7, but these proved relatively inconsequential.

On September 9, a rainfall of 135 mm within 24 hours combined with high tides to flood the marsh to the hammock line so that fish first gained access to the marsh in concurrence with a massive, well-synchronized mosquito hatch, and were free to range at once over the whole marsh. Water stood on the marsh far beyond the next 39 days, although tide levels at the marsh edge (TG₄) fell below marsh ground level, and only occasionally rose above marsh water level. The marsh water level subsided to marsh ground level on September 18 and 27. Following the drought, water temperatures were moderate. The average of the means during each day's collecting was 28.4° C (av. max., 29.9° C, av. min., 27.0° C). Salinities fell below 20 ‰ during and just after heavy rainfall, but rose almost to ocean salinity in large ponds and above it in small ponds during inter-luvial periods.

FISHES INVADING THE MARSH AND SELECTION OF SPECIMENS

Between September 10 and October 17, 8,526 fish of the following 16 species were taken on the marsh (Table I): tenpounder or ladyfish, *Elops saurus* Linnaeus; tarpon, *Megalops atlantica* Valenciennes; rainwater killifish, *Lucania parva* (Baird and Girard); marsh killifish, *Fundulus confluentus* Goode and Bean; Gulf killifish, *F. grandis* Baird and Girard; longnose killifish, *F. similis* (Baird and Girard); Rivulus, *Rivulus marmoratus* (Poey); sheepshead killifish or sheepshead minnow, *Cyprinodon v. variegatus* (Lacépède); eastern mosquitofish, *Gambusia affinis holbrooki* Girard; sailfin or sailfin molly, *Mollienesia latipinna* LeSueur; striped mullet, *Mugil cephalus* Linnaeus; tidewater silverside, *Menidia beryllina* (Cope); snook, *Centropomus undecimalis* (Bloch); striped mojarra, *Diapterus plumieri* (Cuvier); fat sleeper, *Dormitator macu-*

TABLE I. Numbers of fishes taken from the marsh

Method	NUMBERS OF FISH PER METHOD				AVERAGE NO. OF FISH PER COLLECTION			
	Trap	Seine	Poison	All	Trap	Seine	Poison	All
No. of collections	88	25	4	117	88	25	4	117
<i>Elops saurus</i>	2	27	4	33	.02	1.08	1.00	.28
<i>Megalops atlantica</i>	10	192	52	254	.11	7.68	13.00	2.17
<i>Lucania parva</i>	914	17	1	932	10.39	.68	.25	7.97
<i>Fundulus confluentus</i>	82	—	6	88	.93	—	1.50	.75
<i>Fundulus grandis</i>	73	7	10	90	.83	.28	2.50	.78
<i>Fundulus similis</i>	—	3	—	3	—	.12	—	.03
<i>Rivulus marmoratus</i>	2	—	—	2	.02	—	—	.02
<i>Cyprinodon v. variegatus</i>	1673	306	7	1986	19.01	12.24	1.75	16.97
<i>Gambusia affinis holbrooki</i>	934	169	36	1139	10.61	6.76	9.00	9.74
<i>Mollienesia latipinna</i>	1215	455	99	1769	13.81	18.20	24.75	15.12
<i>Mugil cephalus</i>	63	1011	50	1124	.72	40.44	12.50	9.61
<i>Menidia beryllina</i>	1	866	—	867	.01	34.64	—	7.41
<i>Centropomus undecimalis</i>	31	118	23	172	.35	4.72	5.75	1.47
<i>Diapterus plumieri</i>	51	2	1	54	.58	.08	.25	.46
<i>Dormitator maculatus</i>	3	—	—	3	.03	—	—	.03
<i>Evorthodus lyricus</i>	10	—	—	10	.11	—	—	.09
Totals/Averages.....	5064	3173	289	8526	57.55	126.80	72.25	72.87

latus (Bloch); and lyre goby, *Evorthodus lyricus* (Girard).

In 88 trap settings, 5,064 fish of 15 species were taken, in 25 seinnings, 3,173 fish of 12 species, and in 4 spot treatments with rotenone, 289 fish of 11 species (Table I). In the past, *Fundulus similis*, *Menidia*, *Diapterus*, *Dormitator*, and *Evorthodus* had proved uncommon in this habitat. Although common, *Fundulus confluentus* and *F. grandis* are difficult to collect by conventional methods in small clearings among pneumatophores or with unbaited traps; *Rivulus marmoratus* is rare (Harrington and Rivas 1958). At other times some 25 additional species had been taken in Indian River embayments bordering the marsh, but of these only white mullet, *Mugil curema* Valenciennes, hogchokers, *Trinectes maculatus fasciatus* (Lacépède), and the mojarra, *Gerres cinereus* (Walbaum) and *Diapterus olisthostomus* (Goode and Bean), had been taken on the marsh itself. If any of these entered the marsh this time, it was in small numbers.

Aside from tarpon reserved for other purposes, the gut contents of all individuals of a species were analyzed if the total number was not over 400. Fish of all standard lengths available each date were used. The selection of specimens as to standard length was a compromise between an equitable daily length representation and the over-all length representation. Table II gives the collection-date and standard-length distributions of the 2,786 fish examined for food. Despite selection for equitable sampling of larger sizes, 96% of the fish fell within a range of 5 cm in standard length (5-55 mm). This does not ex-

clude the possibility that still larger individuals were on the marsh but selected against by chief reliance on trapping, but this had no support from visual observation, seining, or spot treatment with rotenone.

SYNOPSIS OF THE TOTAL FOOD TAKEN BY ALL FISH SAMPLED

Table III lists all food items collectively for the 2,786 fish. As the itemized cornucopia of organisms of proven availability to the fishes on the marsh, it constitutes the salt-marsh menu relevant to fish. Five categories of food comprised 95% of the volume of the pooled gut contents of all fish sampled: plant materials, 35.79%, *Aedes* mosquitoes, 23.76%, copepods, 14.69%, fishes, 12.52%, and *Palaemonetes* shrimp, 7.80%. The remaining 5% included 69 of the 83 irreducible categories of organisms identified. Plant materials, mosquitoes, and copepods had also the highest frequencies of occurrence. Fishes and *Palaemonetes* belong among the chief fish foods despite their lower frequencies of occurrence, which proved to be functions of predator-prey size ratio as well as of predator inclination. With minor exceptions, the task of discriminating among fishes as to foods eaten is reduced, in effect, to a search for differential selection among and within these 5 categories of food.

As used here, plant debris refers to macerated plant materials that could not be identified; residue includes sand and organic materials of indeterminate origin. Most of the plant volume was vascular tissue, followed by debris and algae, in that order. A high percentage of fish had in-

TABLE II. Collection-date and mm standard-length distributions of fishes examined

	<i>Elops saurus</i>	<i>Megalops adansonii</i>	<i>Lucania parva</i>	<i>Fundulus confluentus</i>	<i>Fundulus grandis</i>	<i>Fundulus similis</i>	<i>Rivulus marmoratus</i>	<i>Cyprinodon v. variegatus</i>	<i>Gambusia a. holbrooki</i>	<i>Mollenesia latipinna</i>	<i>Mugil cephalus</i>	<i>Menidia beryllina</i>	<i>Centropomus undecimalis</i>	<i>Diapterus plumieri</i>	<i>Dormitor maculatus</i>	<i>Evorthodus lyneus</i>	Totals
Totals	33	231	400	88	90	3	2	400	400	400	400	100	172	54	3	10	2786
September																	
10	—	15	7	—	3	1	—	32	26	30	62	—	6	—	—	—	182
11	2	1	37	3	8	2	—	39	31	29	5	100	—	—	—	3	261
12	1	16	33	3	—	—	—	34	30	30	61	—	1	3	—	2	214
13	—	—	25	4	—	—	—	19	11	28	—	—	—	—	1	1	89
14	—	—	33	2	4	—	—	32	16	30	5	—	4	1	—	—	127
15	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
16	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1
17	4	5	33	19	3	—	1	32	30	30	45	—	4	4	—	—	210
18	13	32	23	1	4	—	1	32	30	30	61	—	29	—	—	—	256
19	—	—	31	6	3	—	—	32	30	29	3	—	6	1	—	—	141
21	—	—	33	7	1	—	—	32	30	29	13	—	9	5	1	—	160
26	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1
27	—	—	34	11	15	—	—	25	25	30	—	—	1	10	—	1	152
28	10	72	42	6	13	—	—	35	47	33	61	—	65	5	—	—	389
October																	
1	3	43	34	13	13	—	—	32	30	29	63	—	20	16	—	2	298
3	—	8	34	7	13	—	—	17	25	29	—	—	3	9	—	1	146
10	—	39	—	3	—	—	—	—	22	2	—	—	—	—	—	—	66
11	—	—	—	2	—	—	—	1	6	5	—	—	—	—	—	—	14
17	—	—	1	1	10	—	—	6	11	7	20	—	22	—	—	—	78
S.L.																	
5-15	—	—	49	5	16	3	—	77	69	132	9	100	32	15	1	—	508
16-25	5	106	251	16	16	—	1	166	249	95	368	—	83	36	—	—	1392
26-35	5	82	100	22	24	—	1	121	62	98	21	—	49	2	—	—	587
36-45	6	26	—	28	17	—	—	35	20	42	—	—	8	1	—	2	185
46-55	7	8	—	16	9	—	—	1	—	24	—	—	—	—	1	—	71
56-65	5	3	—	1	1	—	—	—	—	9	—	—	—	—	—	3	22
66-75	3	3	—	—	5	—	—	—	—	—	—	—	—	—	1	—	12
76-85	2	2	—	—	2	—	—	—	—	—	—	—	—	—	—	—	6
101- 7	—	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	2
124	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1
Empty	—	—	35	20	21	—	1	10	20	14	1	—	5	—	—	3	130

gested algae but in small amounts; the few herbivores had consumed mostly vascular tissue, so that the debris probably derives largely from vascular plants. The likeliest source of vascular tissue is the litter of decomposing leaves and other parts of black mangroves and *Batis*. Epidermal layers and epiphytic algae of submerged roots and stems of *Batis maritima* are grazed upon by fishes in Hawaiian fish ponds (Hiatt 1947). It was not possible to distinguish volumetrically among sources of vascular tissue, but leaf glands of *Avicennia* and tissue structurally like that of *Batis* but not of *Salicornia* were recognized in the food. The poor preservation of algae allowed no more than superficial treatment. The cyanophytes and chlorophytes were mostly filamentous, but non-filamentous forms belonging to the Chroococcales and Volvocales were conspicuous. The diatoms were mostly naviculoid, but discoid Coscinodiscineae were also prominent.

The copepods, including eggs and nauplii, were predominantly cyclopoids, comprising about 13.78%, most of the 14.69% contributed by all copepods. Harpacticoids were found in a high percentage of fish, but in small amounts; calanoids were found in minute amounts and in few fish. All intact shrimp were *Palaemonetes intermedius* Holthuis, which on occasion contributed heavily to the food volumes of certain fishes, but occurred in a low percentage of fish and sporadically. Of the invertebrates yet to be considered, exclusive of insects, only gammarideans made up as much as 0.29%. Among these were talitrids of the genus *Hyale* and of 2 species of *Orchestia* and fragments of nontalitrids.

Of 14,981 *Aedes* mosquitoes sampled from the gut contents, 94.4% were *A. taeniorhynchus* and 5.6% were *A. sollicitans*. Accurate counts per fish or conversion of volumes into counts are not feasible, because the head capsule diagnostic of

TABLE III. Percentage frequencies of occurrence and percentages of the aggregate volume of all organisms in the alimentary tracts of the 2,786 fish sampled

Item	% vol.	% freq.	Item	% vol.	% freq.	Item	% vol.	% freq.
PLANT	35.79	34.28	Collembola	.01	1.22	Chironomidae	.01	1.08
Debris	7.38	5.89	Orthoptera	.17	.11	Ceratopogonidae	.03	3.02
Vascular	25.98	3.15	Psocoptera	.01	.25	unidentified	.02	2.58
Algae	2.42	19.92	Thysanoptera	T	.25	Culicoides	.01	.39
Chlorophyta	1.08	8.44	Hemiptera	.38	4.99	Dasyhelina	T	.04
Diatoms	.04	14.75	unidentified	.01	.65	Sciaridae	T	.04
Cyanophyta	1.30	11.56	Homoptera	.22	2.69	Cecidomyiidae	T	.39
Arcella	T	3.45	unidentified	T	.18	Stratiomyiidae	T	.04
Diffugia	T	2.87	Cicadellidae	.20	.83	Tabanidae	.05	.36
Globigerina	T	4.52	Coccoidea	.02	1.76	Dolichopodidae	.08	.36
Rotifera	T	1.54	Chermidae	T	.04	Syrphidae	.05	.25
Nematoda	T	.22	Heteroptera	.15	1.94	Muscoidea	.02	.11
Annelida	.02	1.18	Veliidae	.03	.18	Ephydriidae	.01	.07
Gastropoda	.03	2.15	Corixidae	.12	1.79	Coleoptera	.23	2.84
Crustacean fragments	.05	.86	nymphs	.12	1.36	fragments	.08	1.33
Cladocera	T	1.01	eggs	T	.07	Carabidae	.01	.04
COPEPODA	14.69	64.25	Lepidoptera	.02	.39	Hydrophilidae	.12	1.97
fragments	T	1.62	Diptera unidentified	.10	1.18	Limnebiidae	.01	.47
Calanoida	.06	2.19	Orthorhapha unident.	.02	.04	Ptilidae	.01	.83
Cyclopoida	12.64	42.03	Cyclorhapha unident.	.17	1.51	Hymenoptera	.11	3.05
Harpacticoida	.76	37.87	Tipulidae	.01	.43	fragments	T	.07
nauplii	.39	18.27	Psychodidae	T	.04	Formicoidea	.09	2.40
eggs	.84	38.12	Culicidae	—	—	Chalcidoidea	.02	.86
Branchiura (Argulus)	T	.04	Anopheles	.01	.14	Pseudoscorpionida	T	.04
Ostracoda	.01	1.72	AEDES	23.76	43.04	Araneida	.14	1.54
Isopoda	.17	.80	fragments	.14	8.26	Acarina	.01	7.72
Gammaridea	.29	1.72	1st instar	1.39	.95	Symphyla	T	.07
PALAEMONETES adults	7.72	2.30	2nd instar	1.49	9.73	Arthropod fragments	.18	28.57
zoeca	.08	1.22	3rd instar	5.24	13.53	Invertebrate eggs	.34	11.38
Crab zoeca	.09	4.67	4th instar	10.90	13.10	FISHES	12.52	9.05
Insect fragments	.46	10.34	pupae	4.01	7.90	Residue	1.95	29.61
Thysanura	T	.04	adults	.58	.97	Above trace items (T)	.21*	—

* Each trace item (T) comprised less than 0.01% of the aggregate food volume.

instar and the siphon and comb scales diagnostic of both instar and species often become detached from the rest of the body. Further mention of mosquitoes implies both species in about the above proportions.

Insects other than *Aedes* mosquitoes formed 1.95% of the total food volume, bringing the contribution of insects to about 25%. Toward the last of September, the emergence and exodus of the *Aedes* brood reduced the hitherto overwhelming numbers of mosquitoes below the numbers of all other insects. The small contribution of the latter (1.95%) to the total food volume suggests that few fishes then turned to feeding on alternate insect taxa.

In addition to mosquitoes, most of the other insects eaten belong to groups with halophilic representatives, viz. Collembola, Heteroptera (veliids, corixids), Diptera (tipulids, chironomids, ceratopogonids, stratiomyiids, tabanids, dolichopodids, ephydriids), Coleoptera (carabids, hydrophilids, limnebiids), and some chalcidoid hymenopterans (mymarids) with swimming adaptations (*cf.* Bertrands 1954, Gunter and Christmas 1959, Hutchinson 1931, Johannsen 1935, 1937, Pearse 1950,

Remane and Schlieper 1958, Rogers 1932, Ségué 1950, Usinger 1957, Young 1954). Among the hydrophilids were *Enochrus* sp. and *Tropisternus* sp., and among the limnebiids, probably *Ochthebius* sp. Among the corixids was *Trichocorixa* sp. Terrestrial arthropods from the vegetation canopy were also taken, among them bark lice (Psocoptera: Psyllipsocidae), ants and spiders.

The fish were usually well digested; those identified were mostly young *Mollienesia latipinna*, many of them neonates, the rest, small *Gambusia a. holbrooki*.

SYNOPSIS OF FOOD BY FISH SPECIES

The gut contents of the 11 best represented fishes are analyzed in Tables IV-V. Table IV gives the percentage contributed by each item to the pooled food volume of all fish sampled per species. The contribution of each item is recorded to the nearest percent; those contributing less than 1% are summed as miscellaneous items. Table V gives the percentage frequencies of occurrence of each item consumed by 10% or more of at least one species of fish; the frequencies are recorded to the nearest percent. Items nominally excluded

from these tables are of little importance (*cf.* Tables III-V). Assorted invertebrate (mostly insect) eggs made up as much as 1% of the total food volumes only of *Cyprinodon* and of *Gambusia*. The volume of residue was negligible in all fishes but *Mugil* (7%), and was largely sand only in the case of *Cyprinodon*.

TABLE IV. Percentages contributed by each item to the aggregate food volume per fish species. Each item is recorded to the nearest %. Those comprising less than one % are summed in the last category

Fish species*	<i>Elops saurus</i>	<i>Megalops atlantica</i>	<i>Lucania parva</i>	<i>Fundulus confluentus</i>	<i>Fundulus grandis</i>	<i>Cyprinodon v. variegatus</i>	<i>Gambusia a. holbrooki</i>	<i>Mollienesia latipinna</i>	<i>Mugil cephalus</i>	<i>Centropomus undecimalis</i>	<i>Diapterus plumieri</i>
Number of fish	33	231	400	88	90	400	400	400	400	172	54
PLANT.....	—	—	—	1	2	58	8	64	61	—	—
Debris.....	—	—	—	—	—	—	—	—	51	—	—
Vascular.....	—	—	—	1	2	52	8	62	7	—	—
Algae.....	—	—	—	—	—	6	—	2	2	—	—
Chlorophyta.....	—	—	—	—	—	4	—	—	—	—	—
Diatoms.....	—	—	—	—	—	—	—	—	1	—	—
Cyanophyta.....	—	—	—	—	—	2	—	2	—	—	—
Annelida.....	—	—	—	4	1	—	—	—	—	—	—
COPEPODA.....	17	82	32	—	—	9	—	24	4	89	—
Cyclopoida.....	16	82	22	—	—	7	—	14	4	80	—
Harpacticoida.....	—	—	9	—	—	2	—	2	6	—	—
Nauplii.....	—	—	—	—	—	—	—	2	—	—	—
eggs.....	—	—	—	—	—	—	—	5	—	3	—
Isopoda.....	—	—	6	3	—	1	—	—	—	—	—
Gammaridea.....	—	—	—	—	—	—	—	—	—	—	—
PALAEONETES.....	44	3	1	19	64	1	1	—	8	—	—
Orthoptera.....	—	—	—	—	—	—	3	—	—	—	—
Hemiptera.....	—	—	1	—	1	—	5	—	—	—	—
Aedes mosquitoes.....	1	5	51	54	17	38	52	31	7	—	9
1st instar.....	—	—	3	—	1	2	3	1	2	—	—
2nd instar.....	—	—	8	—	—	3	2	1	—	—	—
3rd instar.....	—	—	19	1	1	10	6	7	4	—	8
4th instar.....	—	4	13	30	—	17	21	18	—	—	—
pupae.....	—	—	9	17	9	6	17	3	—	—	—
adults.....	—	—	—	5	5	—	2	—	—	—	—
Dolichopodidae.....	—	—	—	3	—	—	—	—	—	—	—
Syrphidae.....	—	—	1	—	—	—	—	—	—	—	—
Coleoptera.....	—	—	1	1	1	—	2	—	—	—	—
Formicoidea (ants).....	—	—	—	—	—	—	1	—	—	—	—
Araneida.....	—	—	—	—	1	—	2	—	—	—	—
Invertebrate eggs.....	—	—	—	—	—	1	1	—	—	—	—
FISHES.....	37	9	—	8	10	—	5	—	88	—	—
Residue.....	—	—	1	2	—	1	—	3	7	—	—
Miscellaneous.....	1	1	6	4	2	1	10	2	1	—	1

* Poorly represented fishes considered in the text: *Pundulus similis*, *Rivulus marmoratus*, *Menidia beryllina*, *Dormitator maculatus*, and *Evothodius lyricus*.

TABLE V. Percentage frequencies of occurrence per fish species of each food item with a frequency of occurrence of 10% or more in at least one species of fish

Fish species*	<i>Elops saurus</i>	<i>Megalops atlantica</i>	<i>Lucania parva</i>	<i>Fundulus confluentus</i>	<i>Fundulus grandis</i>	<i>Cyprinodon v. variegatus</i>	<i>Gambusia a. holbrooki</i>	<i>Mollienesia latipinna</i>	<i>Mugil cephalus</i>	<i>Centropomus undecimalis</i>	<i>Diapterus plumieri</i>
Number of fish	33	231	400	88	90	400	400	400	400	172	54
PLANT.....	15	2	7	10	14	67	13	67	63	13	13
Debris.....	—	—	—	—	—	8	—	—	1	32	—
Vascular.....	9	1	4	9	12	61	13	64	62	12	13
Algae.....	3	1	4	5	3	41	2	42	45	2	—
Chlorophyta.....	3	1	4	3	3	21	1	15	15	1	—
Diatoms.....	3	—	1	1	—	21	1	31	44	1	—
Cyanophyta.....	—	—	—	—	—	19	1	21	39	1	—
Arcella.....	—	—	—	—	—	4	—	1	18	1	—
Globigerina.....	3	1	1	2	3	10	—	9	9	1	1
COPEPODA.....	91	99	74	30	37	48	60	23	81	73	87
Calanoida.....	9	1	—	—	1	—	1	—	3	22	4
Cyclopoida.....	85	97	55	14	23	11	35	5	67	56	83
Harpacticoida.....	39	37	53	23	26	36	45	18	35	35	76
nauplii.....	6	47	13	—	7	20	12	2	39	5	15
eggs.....	67	91	59	8	17	27	29	3	54	38	70
PALAEONETES.....	21	1	2	5	8	1	4	1	—	18	2
Crab zoeae.....	30	1	6	3	7	4	8	1	1	8	6
Hemiptera.....	3	1	8	1	7	3	16	3	2	—	7
AEDES mosquitoes.....	15	28	39	42	24	70	54	57	40	9	13
1st instar.....	9	10	6	8	7	14	13	8	12	6	9
2nd instar.....	6	1	12	3	9	15	12	10	12	1	6
3rd instar.....	3	2	16	3	7	23	15	18	18	2	2
4th instar.....	3	6	10	26	6	31	19	17	2	—	—
pupae.....	—	—	4	9	4	20	12	11	4	1	2
Coleoptera.....	6	1	4	6	4	6	12	4	2	1	—
Hymenoptera.....	—	—	—	1	8	2	12	4	1	—	—
Acarina.....	—	16	3	2	4	12	11	10	5	2	4
Invertebrate eggs.....	6	1	9	1	4	24	12	18	11	2	4
FISHES.....	39	21	—	5	3	—	3	—	—	56	—
Residue.....	3	—	26	28	24	43	5	73	32	2	4

* See footnote Table IV.

versity of organisms taken without regard to volume are: *Gambusia* (50), *Cyprinodon* (41), *Fundulus grandis* (39), *Lucania* (33), *F. confluentus* (32), *Mollienesia* and *Mugil* (each 27), *Megalops* (21), *Elops* and *Centropomus* (each 18), and *Diapterus* (16), the counts being of an analogous list from Table III. *Gambusia*, *Fundulus confluentus*, *F. grandis*, and *Lucania* top both series. Although *Cyprinodon* ranks high as determined by percentage frequencies of occurrence, it ranks low as determined by percentage volumes, and was an essentially restricted feeder.

A more objective and succinct expression of the interrelated food habits of these fishes is obtained by ranking them within different feeding categories. The pattern abstracted from these data applies to the salt marsh and in other habitats departures are to be expected from it. *Elops*, *Megalops*, *Mugil*, *Centropomus*, and *Diapterus* grow much larger than their representatives on the marsh, which included very early stages. Some of them showed dietary changes within the size ranges on the marsh. *Elops* and *Megalops* are starred below to emphasize that, al-

The ranks of these fishes as to diversity of organisms taken in amounts of 1% or more of the total food volumes are: *Gambusia* (12), *Fundulus confluentus* and *F. grandis* (each 9), *Lucania* (8), *Cyprinodon*, *Mugil*, and *Diapterus* (each 5), *Elops* and *Megalops* (each 4), *Mollienesia* and *Centropomus* (each 3), the counts being of all items as listed in Table IV except the following as named: Plant, Chlorophyta, Diatoms, Cyanophyta, Copepoda, instars 1-4, pupae, adults, Residue, and Miscellaneous. Their ranks as to di-

1) Herbivores			2) Plankton eaters		
Criterion: total plant (continuous availability)			Criterion: cyclopoid copepods (continuous availability)		
<i>Mollienesia</i>	64	67	<i>Megalops</i>	82	97
<i>Mugil</i>	61	63	<i>Diapterus</i>	80	83
<i>Cyprinodon</i>	58	67	<i>Lucania</i>	22	55
<i>F. grandis</i>	2	14	<i>Elops</i>	16	85
<i>F. confluentus</i>	1	10	<i>Mugil</i>	14	67
<i>Elops</i>	Trace	15	<i>Gambusia</i>	7	35
<i>Gambusia</i>	Trace	13	<i>Centropomus</i>	4	56
<i>Centropomus</i>	Trace	13	<i>F. grandis</i>	Trace	23
<i>Diapterus</i>	Trace	13	<i>F. confluentus</i>	Trace	14
<i>Lucania</i>	Trace	7	<i>Cyprinodon</i>	Trace	11
<i>Megalops</i>	Trace	2	<i>Mollienesia</i>	Trace	5
3) Larvivores			4) Piscivores		
Criterion: total <i>Aedes</i> (transitory predominance)			Criterion: total fish (continuous availability with a size effect)		
<i>F. confluentus</i>	54	42	<i>Centropomus</i>	88	56
<i>Gambusia</i>	52	54	* <i>Elops</i>	37	39
<i>Lucania</i>	51	39	* <i>Megalops</i>	9	21
<i>Cyprinodon</i>	38	70	<i>F. grandis</i>	10	3
<i>Mollienesia</i>	31	57	<i>F. confluentus</i>	8	5
<i>F. grandis</i>	17	24	<i>Gambusia</i>	5	3
<i>Diapterus</i>	9	13			
<i>Mugil</i>	7	40			
<i>Megalops</i>	5	28			
<i>Elops</i>	1	15			
5) Nonpiscivores (unranked)			6) Diverse feeders (ranked)		
<i>Lucania</i>			<i>Gambusia</i>		
<i>Cyprinodon</i>			<i>F. confluentus</i>		
<i>Mollienesia</i>			<i>F. grandis</i>		
<i>Mugil</i>			<i>Lucania</i>		
<i>Diapterus</i>					
7) Restricted feeders (ranked)					
<i>Centropomus</i>					
<i>Elops</i>					
<i>Megalops</i>					
<i>Mollienesia</i>					
<i>Diapterus</i>					
<i>Mugil</i>					
<i>Cyprinodon</i>					

though both belong with *Centropomus* as the chief piscivores, *Megalops* was better represented in our collections by the smaller and *Elops* by the larger sizes present on the marsh. The other 6 fishes are well represented from very small individuals to definitive size.

The organisms consumed by the 5 fishes uncommon on the marsh (Table II and Table IV, footnote) may now be recorded volumetrically. The 3 *Fundulus similis* contained 2% cyclopoid copepods, 2% harpacticoid copepods, 76% *Aedes*

mosquitoes (instars 1-2), 19% undetermined dipteran (Cyclorapha) larvae and pupae, and 1% residue. The emphasis on mosquitoes allies this fish with the other species of *Fundulus*. The two *Rivulus marmoratus* had taken only mosquitoes (4th instar, 60%; pupae, 40%). The 100 *Menidia beryllina* were early stages taken at one site the same day (Table II). These contained 0.5% vascular plant tissue, 1% diatoms, 12% *Diffugia*, 8% gastropods, 3% cladocerans, 38% copepods (15% cyclopoids, 20% harpacticoids,

2% nauplii, and traces of calanoids and eggs), 1% crab zoeae, 3% *Aedes* mosquitoes (mostly 2nd instar), 1% coleopterans (limnebiids), 1% insect eggs, about 30% combined arthropod fragments and residue, and traces of collembolans,

thysanopterans, ceratopogonids, and mites. Fish of this species hitherto examined for food (Hildebrand and Schroeder 1928, Reid 1954, Darnell 1958) were much larger, but Darnell surmised an earlier zooplankton-feeding stage preying large-

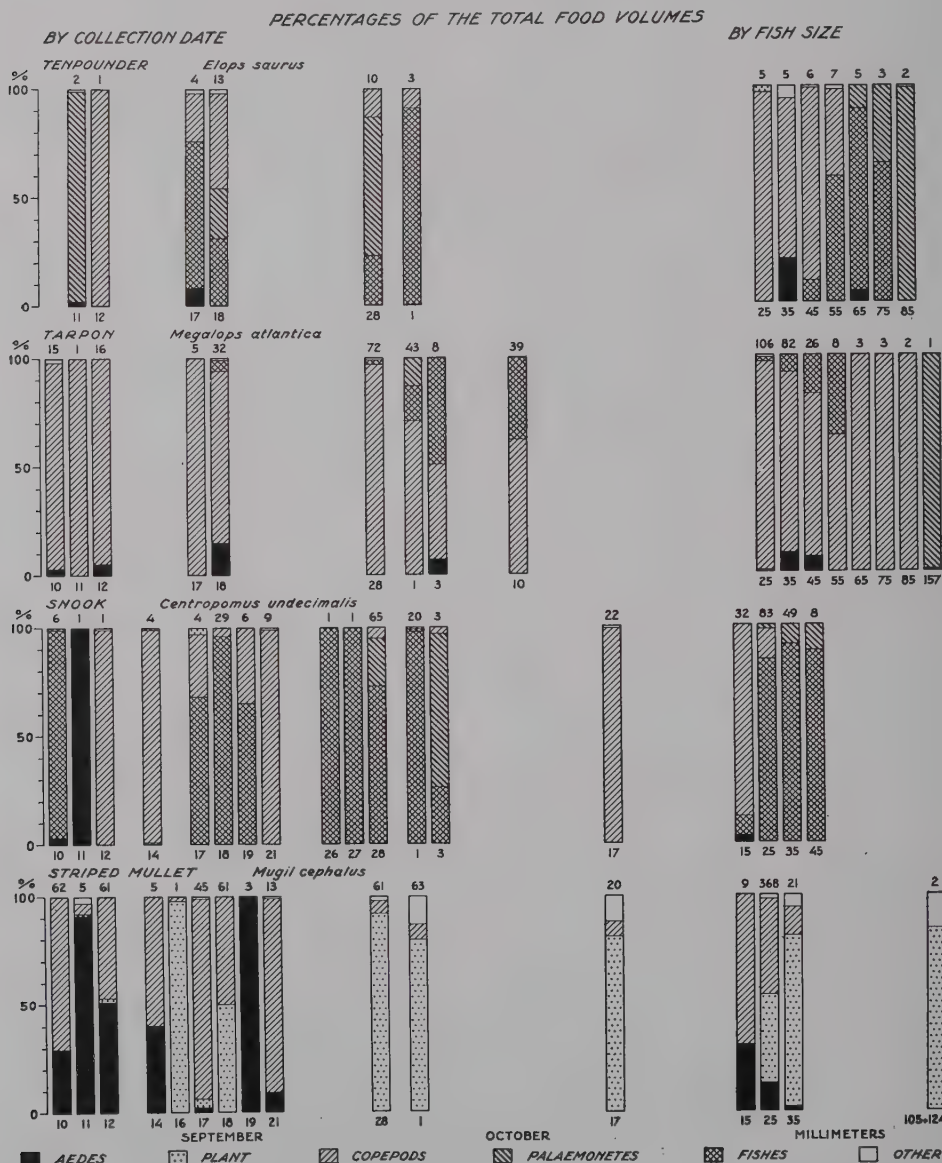


FIG. 3. Percentage contributions of the 5 major items to total food volumes of *Elops saurus*, *Megalops atlantica*, *Centropomus undecimalis*, and *Mugil cephalus*. To the left: by date; to the right: by fish size. Numbers of fish above each bar; dates or standard lengths below; 15 mm refers to 5-15 mm, 25 mm, to 16-25 mm, etc.

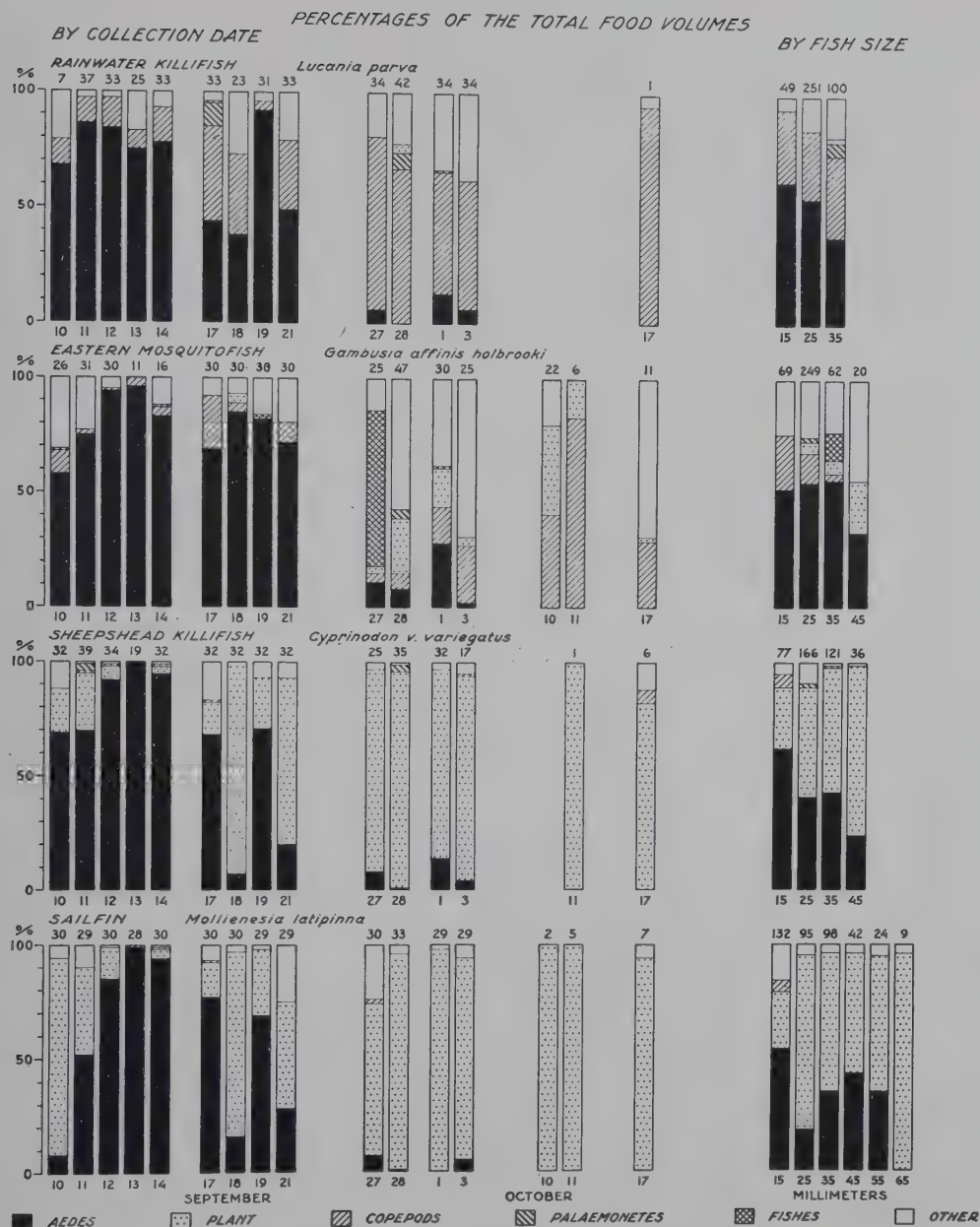


FIG. 4. Percentage contributions of the 5 major items to total food volumes of *Lucania parva*, *Gambia affinis holbrooki*, *Cyprinodon variegatus variegatus*, and *Mollienesia latipinna*.

ly on calanoid copepods, which agrees in general if not in detail with the present food analysis. The 3 sleepers, *Dormitator maculatus*, had taken 99% *Aedes* mosquitoes (4th instar, 96%; 3rd instar, 3%; and traces of pupae), and 1% cyclopoid copepods, isopods, and arthropod frag-

ments. This species is listed as a mosquito-eating fish (Anonymous 1924), but its life history is obscure. The 10 specimens of *Evorthodus lyricus* had consumed 84% algae (mostly cyanophytes, with some diatoms and chlorophytes), 15% *Aedes* mosquitoes, and 1% ceratopogonids and insect

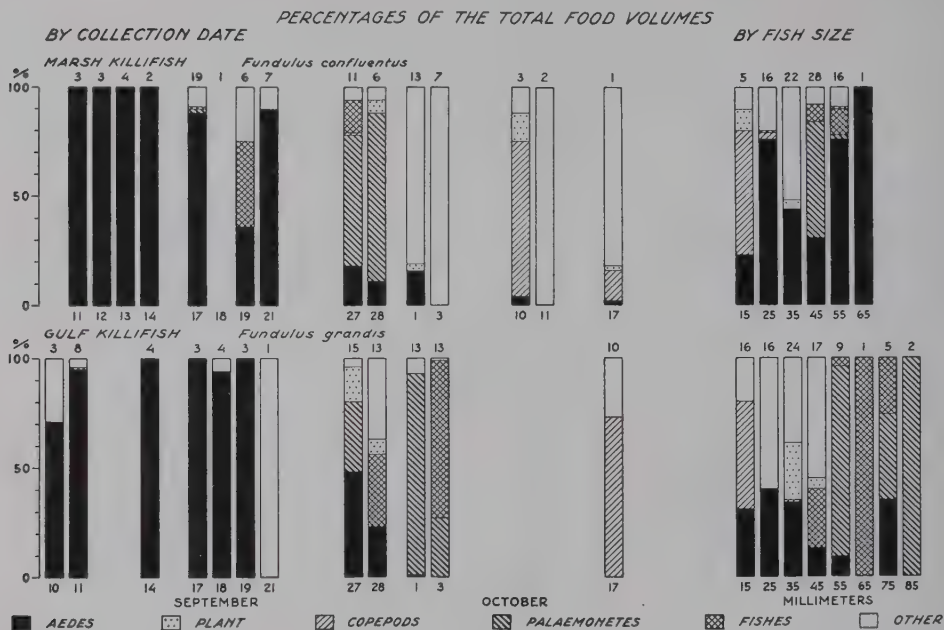


FIG. 5. Percentage contributions of the 5 major items to total food volumes of *Fundulus confluentus* and *Fundulus grandis*.

eggs. These 5 fishes and *Diapterus plumieri* deserve no further attention as they are of uncertain status and uncommon on such marshes.

DIETS COMPARED DURING CHANGING FOOD AVAILABILITY WITH RESPECT TO FISH SIZE

Figures 3-5 show the percentage volumes of the 5 major food items taken by the 10 commonest fishes on the marsh on successive dates and at successive 10-mm standard-length ranges. The miscellany of subordinate foods is subsumed under the heading "other." Each bar represents 100% of the pooled food volumes of fish collected the same day (to the left) or of the same length class (to the right). Above each bar is the number of fish sampled, and below, either the date or fish size class in mm of standard length. Each standard-length class spans 10 mm, but for lack of space in the figures only the maximum length of each range is given, e.g. 15 refers to 5-15 mm as in Table II.

These fishes fall into 2 groups, those spending their whole lives on or at the fringes of the marsh and the less abundant, immigrant fishes, which spend only a part of their lives in the vicinity of the marsh. The former will be called "area residents," the latter, "transients," and the 6 uncommon fishes, "unclassified." The diets of

the transients, *Elops*, *Megalops*, *Centropomus*, and *Mugil*, contrast with those of the area residents, *Lucania*, *Fundulus confluentus*, *F. grandis*, *Cyprinodon*, *Gambusia* and *Mollienesia*. The transients (Fig. 3), with one exception fed only incidentally on mosquitoes; all the area residents (Figs. 4-5) fed heavily on them during the interval of mosquito abundance, turning primarily to alternate foods only after the mosquito population was depleted by the emergence and exodus of adults or during the temporary drop in marsh water level on September 10 (*Cyprinodon* and *Mollienesia*).

Alone of the transient fishes, the guts of mullet reflected the temporary predominance of mosquitoes, but with increase in size (Fig. 3, to the right) mullet soon forsook the animal diet of mosquitoes and copepods for their better known plant diet. This brief, early, carnivorous phase of *Mugil cephalus* has received little attention, but Ebeling (1957) noted in some species of mullet indications of a change-over from a juvenile browsing or carnivorous habit to an adult ilio-phagous habit. The 33 tenpounders were adequately distributed as to dates and length classes (Table II) to disclose a diet like that of their relative, the tarpon. Both tended to feed on copepods when small and on fishes and *Palaemonetes* when larger. On the basis of more specimens

than examined here, but within the same size range and mostly from the same marsh, *Megalops* had been found to feed mainly on cyclopoid copepods and fish. The two items made up 95% or more of the total food volumes throughout a series of stages from mid-metamorphic larval through young tarpon, the proportion of fishes eaten increasing gradually at the expense of copepods with increase in tarpon size (Harrington and Harrington 1960). The snook diet was similar, but fishes became the staple of very small snook, while *Elops* and *Megalops* reached larger size before turning from copepods to fishes and *Palaemonetes*. This may be a function of the wider gape of young snook.

The 6 area residents were cyprinodontiform fishes. Greater efficacy of one of these avid larvivores over the others would be hard to establish. In contrast to the situation among the transient fishes, latent differences in food preference among the area residents first became patent after the depletion of the mosquito brood. *Cyprinodon* and *Mollienesia* resemble each other and differ from the others in turning then to a preponderantly vegetable diet. They consumed little besides plant materials or mosquitoes, and least among cyprinodontiform fishes of the assorted minor items. In the latter respect they resemble the transient fishes (Fig. 3). The consumption of minor items was essentially confined to the smaller fish (Fig. 4, to the right). The diets of these 2 fishes were indistinguishable volumetrically, but further study might disclose subtle differences indicated by the exceptional diversity of individually scarce items in guts of *Cyprinodon*, which was also the only fish on the marsh that had ingested appreciable amounts of sand.

The 4 remaining cyprinodontiform species continued to be primarily carnivorous. The smallest, *Lucania parva*, reverted to a diet chiefly of copepods, supplemented by minor items. The diversity of minor items increased with increase in fish size, and larger fish also took some *Palaemonetes* and plant materials. Although *Lucania* can hardly be considered stenophagous, *Gambusia*, *Fundulus confluentus*, and *F. grandis* agreed in turning after the mosquito exodus to a greater diversity of alternative food organisms than any other fishes on the marsh, including the highest percentage volumes of minor items. The relative sizes of these 3 fishes are reflected in Table II and in Figures 4-5. Despite their generally similar diets, Figures 4-5 indicate differences, which may be functions of fish size. Copepods contributed most to the food volumes of those 5-15 mm in standard length regardless of species,

Palaemonetes and fishes contributed most to those of the largest species and of the largest individuals of the 2 smaller species. A little plant material was taken by each but most consistently by *Gambusia*.

The question remains as to what extent other insects replaced mosquitoes in the diets of larvivorous fishes after mosquitoes left the marsh. The interval of mosquito superabundance may be taken as September 10 through 21, that of mosquito scarcity, as September 27 through October 17. Within the latter period, those mosquitoes hatched from eggs deposited at the perimeter of the flooded area by changes in marsh water level were few enough to be ignored. Mosquitoes contributed the following percentages to the total food volumes consumed per species from September 10 through 21: *Fundulus grandis*, 94.8%, *F. confluentus*, 85.5%, *Gambusia*, 78.7%, *Lucania*, 72.8%, *Cyprinodon*, 57.3%, and *Mollienesia*, 52.3%. The lower figures for *Cyprinodon* and *Mollienesia* resulted partly from the fall in water level of September 18, the possibly related earlier reversion to their staple (plant) diet, and the initial tardiness with which *Mollienesia* began feeding on mosquitoes. During mosquito scarcity, September 27 to October 17, other insects contributed the following percentages to the total food volumes: *Gambusia*, 32.7% (10 orders, 20 families), *Lucania*, 11.3% (3 orders, 5 families), *Fundulus confluentus*, 9.3% (3 orders, 9 families), *F. grandis*, 3.5% (5 orders, 11 families). *Cyprinodon* and *Mollienesia* ate plant materials.

Of the unspecified foods taken between September 27 and October 17, those exclusive of the insects just considered contributed as follows to the total food volumes: *Fundulus confluentus*, 15.7%, mostly annelids and isopods, with some spiders, gammarideans, nematodes, gastropods, and ostracods, in that order, *Lucania*, 11.5%, mostly gammarideans, isopods, crab zoeae and annelids, with some foraminiferans, mites and ostracods, *Gambusia*, 6.0%, mostly crab zoeae, spiders, gammarideans, and isopods, with some mites, annelids, pseudoscorpions, and gastropods, *Fundulus grandis*, 3.6%, mostly isopods and annelids, with some spiders, gastropods, gammarideans, and mites.

The main trends in food selection among the fishes on the marsh are summarized in Table VI with the insights provided by the contrasts in foods consumed during the peak abundance and during the effectual absence of the overriding food variable, *Aedes* mosquitoes. The nominal categories, omnivorous and benthos feeders, have been

avoided because all of the fishes in a sense are omnivorous and, although the herbivores are obvious benthos feeders, all of the fishes were in very shallow water, where the distinction between benthos and non-benthos feeding is unclear. Of the fishes uncommon on the marsh, *Rivulus*, *Fundulus similis*, and *Evorthodus* were apparently effective larvivores, the last essentially herbivorous, however; *Diapterus* and *Menidia*, of the sizes present, were plankton eaters, *Diapterus* being also a substantial larvivore.

PROGRESS OF THE MOSQUITO BROOD REFLECTED IN THE DIETS OF PREDATORS

Predation on mosquitoes is a complex phenomenon even when considered apart from predation on alternate food organisms. The percentages contributed by the different mosquito stages to the total gut contents of *Lucania*, *Gambusia*, *Cyprinodon*, and *Mollienesia* afford the soundest bases for insights into the problem here, since these

fishes were the best represented in our collections. In Figure 6, the percentages each date refer to the pooled total food volumes of all 4 fishes regardless of species. Figure 7 shows the percentages contributed by each mosquito stage to the daily food volumes of each fish species separately.

The percentage volumes of Fig. 6 reflect the increasing longevity of successive mosquito stages, a well-known trait of mosquito broods (cf. Christophers 1960), although this figure is marred by the lack of data for September 15-16 and by the brief fall in marsh water level of September 18. The contrast between the gut contents of September 18 and those of the day before and of the day after show the deceptiveness of food sampling isolated from the temporal context of ecological change. Evidently, by affecting mosquito availability, the drop in water level, although of short duration, influenced predation on the persisting stages, 4th instar larvae and pupae. *Cyprinodon* and *Mollienesia* (Fig. 7) turned for one day primarily to plant materials (Fig. 4);

PERCENTAGES OF COMBINED TOTAL FOOD VOLUMES BY DATE OF
Lucania, *Gambusia*, *Cyprinodon* and *Mollienesia*

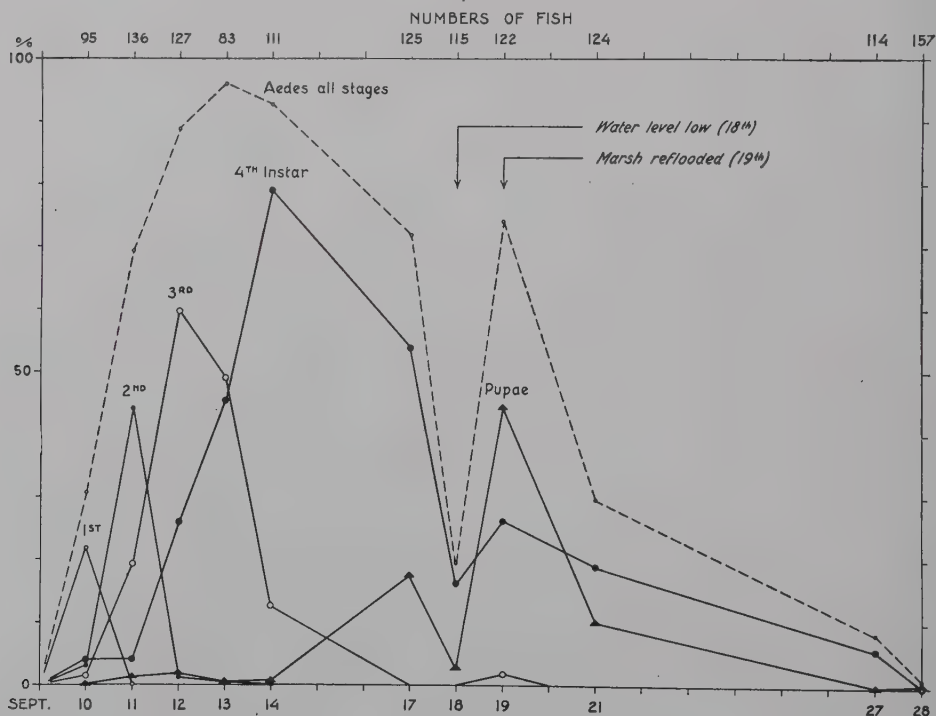


FIG. 6. Percentages contributed by *Aedes* mosquitoes to the combined daily total food volumes of 1600 fish (400 each of *Lucania parva*, *Gambusia affinis holbrooki*, *Cyprinodon variegatus variegatus*, and *Mollienesia latipinna*).

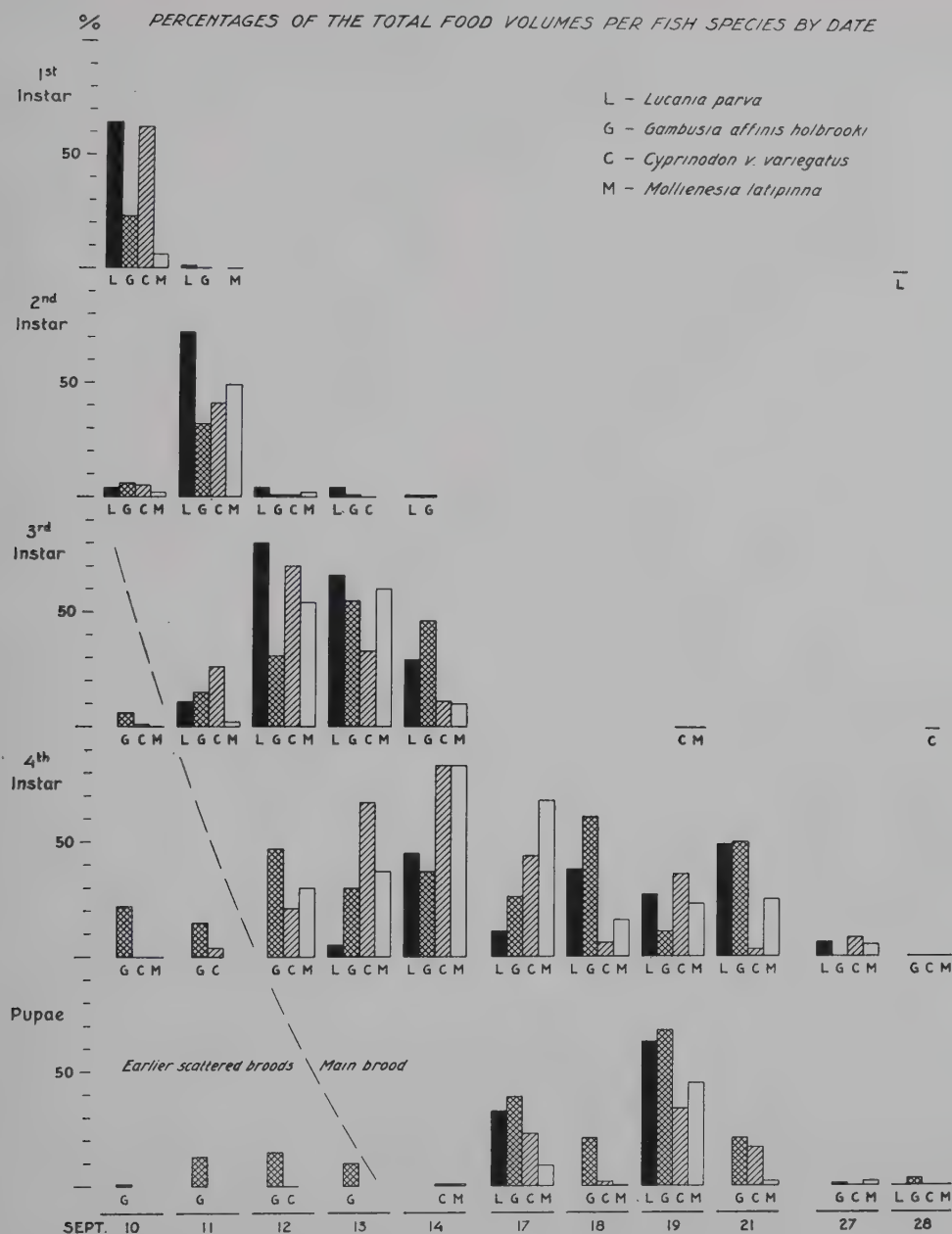


FIG. 7. Percentages contributed by *Aedes* stages to the daily total food volumes of *Lucania parva* (black bars), *Gambusia affinis holbrooki* (crosshatched bars), *Cyprinodon variegatus variegatus* (singly-hatched bars), and *Mollienesia latipinna* (white bars).

Lucania and *Gambusia* were diverted from pupae to 4th instar larvae, both markedly increasing their consumption of larvae on September 18, although on the preceding and following days they were the heaviest predators on pupae.

In addition to changes in water level, the differential availability of successive mosquito stages is inseparable from such factors as time of searching, species-specific searching ability, and degree of ambivalence with respect to accept-

able alternative food organisms. Besides the increasing durations of succeeding larval instars and the much greater sizes of instars 3-4 and pupae compared to those of instars 1-2, the latter tend to be scattered in small patches near former egg deposits, but instars 3-4 aggregate in conspicuous, black sheets, while pupae leave the water surface less often than larvae, and are prone to stranding at low water. The searching time of a predator fish is a hyperbolic function of the prey population density. It increases rapidly at low prey densities, as they approach either zero density or a critical density below which predator-prey interaction breaks down. It reaches its lower limit at a certain high prey density. At prey densities higher than usual in nature, there is also a decline in rate of food consumption as such, apart from time spent searching (Ivlev 1944).

Local prey densities higher than usual in nature are often reached by salt-marsh mosquito broods when 3rd and 4th instars comprise the vanguard of the brood, but are reduced soon after the pupal stage is reached. In the present case (Fig. 6), the pupation peak was reached about the seventh day (Sept. 16) after hatching. The main period of emergence was the 8th through 11th days (Sept. 17-20), with the peak probably on the 9th day. The main exodi, the last of which has been described (Haeger 1960, "brood IV"), occurred on the 9th, 10th, and 11th nights with the peak probably on the 9th night. An interpretation of data of the sort in Figs. 6 and 7 cannot avoid *ex post facto* rationalization, but the above factors clearly allow for diversity in the relative efficiency with which various sizes and species of fish exploit the ontogenetic stages of a mosquito brood in an unstable, multizonal arena.

The performance of *Gambusia* was unique in that it alone exploited the later stages of the small, scattered antediluvial broods (Fig. 7, lower left), which suggests superior searching ability and a predilection for later stages. Although data are lacking for the days of greatest pupal abundance (Sept. 15-16), *Gambusia* and *Lucania* proved the heaviest eaters of pupae, possibly owing to their frequent forays into the shallowest waters. Hess and Tarzwell (1942) found *Gambusia a. affinis* to have a greater preference for pupae than for larvae of insects in general. The lower consumption of 4th instar larvae by *Lucania* may be size-related as this instar is larger than either earlier instars or pupae. The pronounced ambivalence of *Mollienesia* and *Cyprinodon* in taking mosquitoes as against plant materials has been mentioned. The tardy change-over of *Mollienesia* from plant to mosquito feeding and

the comparative alacrity with which both species reverted to their alternative (vegetable) diet partly account for their consumption of proportionately more 4th instar larvae and fewer pupae than the other 2 fishes.

The differential consumption of various mosquito stages was correlated with fish size. Table VII gives the percentages contributed by each mosquito stage to the pooled total food volumes at each size range regardless of species of 1600 fish. These percentages refer to the food taken between September 10 and October 17 by *Lucania*, *Gambusia*, *Cyprinodon* and *Mollienesia*. The proportionately greater consumption of instars 1-3 the smaller the fish, is unmistakable. Fourth instar larvae were taken in the greatest proportions by medium-sized fish. The differential consumption of pupae was correlated with fish species (Fig. 7), but not with fish size (Table VII). The importance of very small fish in mosquito control is supported by the fact that mosquitoes comprised higher percentages of the food volumes of smaller than of larger fish.

TABLE VI. Main feeding trends among fishes on the marsh

Stenophagous	Euryphagous	The principal fish species invading the salt marsh	Larvivorous	Herbivorous	Piscivorous	Nonpiscivorous	Plankton-eating
		AREA RESIDENTS (common to abundant)					
—	X	<i>Lucania parva</i>	X	—	—	X	X
—	X	<i>Fundulus confluentus</i>	X	—	—	—	—
—	X	<i>Fundulus grandis</i>	X	—	—	—	—
X	—	<i>Cyprinodon v. variegatus</i>	X	X	—	X	—
—	X	<i>Gambusia a. holbrooki</i>	X	—	—	—	(X)
X	—	<i>Mollienesia latipinna</i>	X	X	—	X	—
		TRANSIENTS (common)					
X	—	<i>Elops saurus</i>	—	—	X	—	X
X	—	<i>Megalops atlantica</i>	—	—	X	—	X
X	—	<i>Mugil cephalus</i>	(X)	X	—	X	(X)
X	—	<i>Centropomus undecimalis</i>	—	—	X	—	(X)

DISCUSSION

High subtropical salt marshes are typified in one word by crisis, confronting aquatic life with both opportunity and danger. Opportunity lies in the abrupt accessibility of a rich, untapped, free nutrient budget when the marsh is flooded. Nutrients unlocked from plant and other litter by saprobes and by the physical agency of long annual exposure to dryness are not flushed out periodically as in low salt marshes with daily tidal flooding. High marshes locally remain undated after flooding and probably much of the

TABLE VII. The percentages contributed by each mosquito stage to the pooled food volumes of fish of different length classes regardless of species

Standard lengths ¹ (mm)	5-15	16-25	26-35	36-45	46-60	5-60
Numbers of fish	327	761	381	98	33	1600
Instar I.....	6	6	Trace	Trace	None	2
Instar II.....	9	4	3	1	Trace	3
Instar III.....	25	10	9	8	3	9
Instar IV.....	10	12	23	18	13	18
Pupae.....	6	9	6	6	1	6
Total <i>Aedes</i> ²	57	41	42	32	17	38

¹ Of 400 each of *Lucania*, *Cyprinodon*, *Gambusia*, and *Mollienesia*, collected during and after the interval of mosquito abundance.

² Including fragments and the few adults ingested.

free nutrient is consumed on the marsh rather than swept out. This may account in part for the annual influx of young of such fishes as tarpon and snook. The marsh in question has stayed under water with minor fluctuations from as early as August to as late as February. Soon after flooding, short food chains form, as insect and copepod eggs and the like hatch and fishes move in. Danger lies in the eventual drying down of the marsh, when small organisms are stranded and desiccated. The variety of insect eggs in fish guts sampled suggests that halophilic insects besides mosquitoes, as well as copepods, survive exposure *in ovo*, but the local ecology of indwelling invertebrates is little known. Most fish escape before the marsh is fully exposed, but many are trapped in pools and ponds of varying degrees of persistence, where they are menaced by predators and extremes of temperature. Marsh ponds for months often contain tenpounders, tarpon and snook, in addition to several cyprinodontiform fishes. As ponds contract there is also predation by mammals and birds, as attested by a progressive depletion of larger fish and by tracks of raccoons and wood ibises.

The exodus from the marsh of most of the fish may be related to food impoverishment during the retention of standing water, only the first weeks of which are encompassed by this study. Annual flooding with subsequent persistence of standing water results in biotic imbalance not unlike that at the outset of man-made impoundments. The tremendous abundance of mosquito larvae and pupae during their brief tenure on such marshes is inconceivable unless observed; when the brood leaves, mosquitoes are abruptly eliminated from the food web, since salt-marsh mosquitoes do not lay their eggs in water.

The analyses of foods consumed by fishes on the marsh during the first weeks of inundation are more readily construed as indicating avoidance of

competition for food than such competition. During the peak abundance of mosquitoes, the larvivores stand apart as a group in selecting mosquitoes, with little overlap with other common fishes except young mullet in their transitory, juvenile, carnivorous phase. Although these larvivores converged in feeding on mosquitoes, supply was more than equal to demand, and the proportions consumed among mosquito stages point to size-related and species-specific advantages among these fish in capturing different stages. Nor can clear evidence be adduced of competition after depletion of this common food resource, for then the larvivores became segregated as to diet. Two turned to amply abundant plant materials, another to copepods chiefly, and the remaining 3, to a diversity of foods, among which each showed its own selective emphasis despite dietary overlap. Food segregation is open to opposite interpretations, but the seasonal discontinuities in occurrence, sporadic eruption, and the annual peak density of salt-marsh mosquitoes make it likely that the food segregation after the exodus of mosquitoes reflects the more usual and characteristic feeding patterns of these fishes. Kawanabe (1959) has demonstrated a case of food segregation indicative of severe interspecific competition, but in an ecological context the obverse of that here. Food coaction was studied at several localities with proportionately similar food items, but among which there were proportional differences within the assemblages of fishes. Algal-eating cyprinids were displaced from their feeding grounds and forced to depend on terrestrial insects when the algal-feeding and socially dominant Ayu (*Plecoglossus altivelis*) reached high population densities, but returned to their preferred forage grounds when the population density of the Ayu was low. Whatever the competitive status among salt-marsh larvivores, the role of *Gambusia affinis* against *Aedes* mosquitoes has been overvalued because of its reputation as a predator on freshwater anophelines. In the control of salt-marsh mosquitoes by fishes, the primary consideration should be the endemic cyprinodontiform fishes as locally represented rather than any single species.

Of the other fishes on the marsh, the immigrant young of piscivores were scarcely affected by the incidence of mosquitoes, but fed continually on copepods, fishes and palaemonid shrimp. The sustained abundance and availability of the first 2 items negate the likelihood of severe competition among these fast-growing fishes, of which one was consistently piscivorous and the other 2 shifted with increasing size from copepods to fishes and shrimp, one feeding mostly on copepods, the

other on equal proportions of shrimp and fishes. Of the immigrant young of larger fishes, juvenile mullet alone vacillated among mosquitoes, copepods, and plant materials, settling on a plant diet when mosquitoes were gone.

The synthesis of Larkin (1956) in his review of interspecific competition among fresh-water fishes closely applies to this brackish-water assemblage. The fishes of both environments are characterized by plasticity in food selection, omnivorous diets, sharing of common food resources among species, exploitation of food chains at different levels by the same species, quick change-over to alternative diets, ontogenetic food progression in young of larger species, and short food chains. Interaction among brackish-water fishes along Florida east coast lagoons occurs in habitats where pronounced tidal or pluvial flooding tends to be aperiodic. Receding water isolates subpopulations of different combinations of fishes within one or another of these habitats. High water connects them directly or deviously with open waters of the lagoon, allowing escape or repopulation, and impressive immigrations into a vast depopulated area from the lagoon shore have been observed (Harrington and Bidlingmayer 1958). Thus alertness of response to water movement and adaptability to its consequences are paramount for survival in this transitional zone between brackish and fresh water, lagoon and upland. From one habitat to another, salt marsh, mangrove swamp, ditch, shore embayment, drainage canal, and rain-filled swale, food resources vary.

The food segregation interrupted by convergence on mosquitoes would be increased by differences in home range within the gross habitat among these eurytopic larvivores and by their breeding habits, during 9 or more months of the year at 27° North Latitude (Harrington 1959a), which diverge more than their dietary habits. Of the 2 herbivores, *Cyprinodon* is an oviparous, territory-holding nest builder (cf. Raney *et al.* 1953), but *Mollienesia* is a live-bearer unconstrained by oviposition site requirements. Of the euryphagous forms, the only live-bearer, *Gambusia*, is less halophilic (cf. Hiatt 1947) than the larger, ubiquitous, more euryhaline *Mollienesia*. The diminutive *Lucania* favors shallow, weedy shore embayments, where it probably spawns. *Fundulus confluentus* frequents upland parts of marshes; *F. grandis* commutes between marshes and the open shore of the lagoon, where after dark it may be found in large numbers in shallows next to the litter blown against the mangrove pneumatophores at the water's edge. *F. confluentus* ovi-

posits in both brackish water and fresh water, often at the forefront of high waters, where the eggs may be stranded, but remain viable out of water as long as 3 months (Harrington 1959b), hatching in concurrence with mosquitoes when flooded. Breder (1959) has suggested that such eggs may thereby more often escape predation by grubbing mullet and invertebrates. *F. grandis* breeds in shallow water over high shore terraces of the lagoon, and the indications are that its eggs also survive stranding.

SUMMARY

A high salt marsh in subtropical Florida, as it went dry during a severe drought, lost its fishes and accumulated dense deposits of mosquito eggs ready to hatch at annual autumn flooding. An abrupt tidal-pluvial flooding gave fishes sudden access to the whole marsh in concurrence with a massive, synchronized mosquito hatch. Some 8,526 fish of 16 species were collected on the marsh. Foods consumed by the assemblage of invading fishes were compared daily among fishes during the progress through larval and pupal stages, the emergence, exodus, and subsequent absence of the mosquito brood.

The pooled gut contents of 2,786 fish were by volume: 35.7% plant materials (72.7% vascular tissue, 20.6% debris, 6.7% algae), 23.8% *Aedes* mosquitoes (94.4% *A. taeniorhynchus*), 14.6% copepods (96.5% cyclopoids), 12.5% fishes (mostly neonate *Gambusia* and *Mollienesia*), 7.8% shrimp (*Palaemonetes intermedius*). The remaining 5% comprised 69 of the 83 categories of food identified, of which 2% was insects of 10 orders and 29 families, most with halophilic representatives, the rest: *Arcella*, *Diptera*, *Globigerina*, rotifers, nematodes, annelids, gastropods, cladocerans, branchiurans, ostracods, isopods, gammarideans, crab zoeae, pseudoscorpions, spiders, mites, symphylans, invertebrate eggs (mostly insect), unidentified organic residue, and sand.

Based on percentage volumes and frequencies of occurrence of apposite foods, the following fishes ranked high (1) as herbivores: *Mollienesia*, *Mugil*, *Cyprinodon*, in that order, (2) as plankton eaters: *Megalops*, *Diapterus*, *Lucania*, *Elops*, *Mugil*, (3) as larvivores: *Fundulus confluentus*, *Gambusia*, *Lucania*, *Cyprinodon*, *Mollienesia*, *F. grandis*, (4) as piscivores: *Centropomus*, *Elops*, *Megalops*. *Lucania*, *Cyprinodon*, *Mollienesia*, *Mugil*, and *Diapterus* ate no fish. Diverse feeders, in order of rank, were: *Gambusia*, *F. confluentus*, *F. grandis*, *Lucania*; restricted feeders were:

Centropomus, *Elops*, *Megalops*, *Mollienesis*, *Diapterus*, *Mugil*, and *Cyprinodon*.

Of the "transients" (immigrant young of large species), the passage of the mosquito brood was reflected only in the diet of juvenile *Mugil cephalus*, which vacillated among mosquitoes, copepods, and plant materials, settling on the latter when mosquitoes were gone. *Elops saurus*, *Megalops atlantica*, and *Centropomus undecimalis* fed continually on copepods, fishes and shrimp, with size-related progression from copepods to fishes and shrimp, but with different emphases on these foods.

The "area residents" (cyprinodontiform fishes) turned principally to other foods only after the exodus of the mosquitoes. *Cyprinodon v. variegatus* and *Mollienesis latipinna* reverted to a plant diet, differing only in the wide variety of volumetrically scarce items in the diet of *Cyprinodon*. *Lucania parva* turned chiefly to copepods; *Gambusia affinis holbrooki*, *Fundulus confluentus* and *F. grandis*, to a diversity of foods, each showing its own selective emphasis despite dietary overlap. Of the fishes uncommon on the marsh, *Rivulus marmoratus*, *Fundulus similis*, *Dormitator maculatus*, and *Evorthodus lyricus* ate mosquitoes, the latter preferring plant materials; small *Menidia beryllina* were plankton feeders.

During their superabundance, mosquitoes contributed to total food volumes as follows: *F. grandis*, 94.8%, *F. confluentus*, 85.5%, *Gambusia*, 78.7%, *Lucania*, 72.8%, *Cyprinodon*, 57.3%, *Mollienesis*, 52.3%. During mosquito scarcity, other insects contributed as follows: *Gambusia*, 32.7%, *Lucania*, 11.3%, *F. confluentus*, 9.3%, *F. grandis*, 3.5%.

The deceptiveness of isolated food sampling was demonstrated by a one-day fall in water level, affecting food availability, and changing the diets of 4 fishes for a single day, after which they reverted to their previous foods.

There was good correlation between the size of fish and the size of larvae eaten by them; the smaller the fish, the greater the proportion of instars 1-3 eaten; larger fish ate proportionately more 4th instar larvae. Preference for pupae seemed a matter of species preference, and was not correlated with the size of fish eating them.

In the control of salt-marsh mosquitoes by fishes, the primary consideration should be all of the endemic cyprinodontiform fishes as available locally, including the smallest individuals, rather than any single species.

Food coaction among these fishes is discussed with regard to the resources and vicissitudes of

their environment, competition for food, breeding and spatial requirements.

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AN EXPERIMENTAL STUDY OF COMPETITION FOR FOOD IN FISH¹

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INTRODUCTION

The objective of the present study has been to isolate and analyze certain measurable features

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basic to success in competition, and to evaluate their importance. It was decided to establish situations in which fish would have to compete for every particle of food under experimental feeding conditions and try to determine the degree of success of various fish and the conditions related to that success.

While most experimental work on competition has been done with small, easily culturable organisms (Gause 1934, Crombie 1947, Frank 1952), it becomes necessary to pay attention to individual and social behavior when an analysis of discrete acts of competition in vertebrates is attempted. Since the work of Schjelderup-Ebbe (1922) on the social psychology of the domestic fowl, the widespread importance of aggressive behavior in determining the success of individuals has been recognized (Collias 1944). In fish, frequency of nipping (Braddock 1945) or driving (Greenberg 1947) have been used as indicators of dominance. How driving affects the feeding success of an individual is a necessary part of the problem of evaluating the components of competition.

Studies have been made of the quantitative contribution of various factors to dominance. For instance, a statistical analysis of factors which make for success in initial encounter between hens has been published by Collias (1943). That there may be degrees of aggression has been shown by Bennett (1939, 1940), Maslow (1940) and Seward (1945) for different species of homoiotherms. Moreover, intraspecific variations in dominance have been related to success in some act such as mating (Guhl 1941, Guhl *et al.* 1945) or feeding (Maslow and Flauzbaum 1936) and, in the green sunfish *Lepomis cyanellus*, Alee *et al.* (1948) found a low but highly significant correlation between growth and frequency of drives. In this paper emphasis has been placed on a quantitative analysis of aggressive behavior and feeding success in relation to measurable morphological characteristics.

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CALCULATION OF PERCENTAGE AND CONDITION COEFFICIENT

With data obtained from paired fish, the percentage weight of larger fish for example, was calculated from the formula, $\frac{100 W_1}{W_1 + W_2}$, where

W_1 and W_2 are the weights of the larger and the smaller of two matched fish, respectively.

For fish matched in trios, the following formulae were used:

$$\frac{100 W_1}{W_1 + W_2 + W_3}, \frac{100 W_2}{W_1 + W_2 + W_3}, \text{ and } \frac{100 W_3}{W_1 + W_2 + W_3}.$$

Other percentage calculations such as percentage relative condition coefficient and percentage flies eaten were patterned after the formulae given above for percentage weight.

The relative condition coefficient (Le Cren 1951) was used as a measure of plumpness and is abbreviated to K_n in this paper. It is calculated from the formula, $K_n = W/aL^r$, where W is weight, L is length, and a and r are constants.

EXPERIMENT I.

COMPETITION BY YOUNG SALMON IN PAIRS WITH DIFFERENT FEEDING TECHNIQUES

The fish used in this experiment were hatchery coho salmon, *Oncorhynchus kisutch* (Walbaum), "runt stock," 5.3 to 9.5 cm in fork length and slightly over one year old. Pairs of fish were randomly selected and placed in 14 gallon tubs ($12 \pm 1^\circ\text{C}$), one fish per tub, where they remained without handling until the completion of the experiment. For conditioning feedings, each fish was separated by clear glass partitions and fed individually 5 fruit flies, *Drosophila virilis* Sturtevant, per gram weight of fish. Fish were fed until the majority were eating regularly and those that would not feed were omitted from the final experimental feedings. This practice assured that the results would not be confused by sick or non-feeding fish. The partitions were removed at least 3 hours before experimental feedings to permit contact between fish.

For experimental feedings in which fish were fed flies offered at random intervals, etherized, vestigial-winged flies, *D. melanogaster* (Meigen), were placed on plastic dishes suspended over the water. On recovering they jumped or fell at random, one by one, into the water.

The number of vestigial-winged flies placed on the dishes varied with the aggregate weights of matched fish, 10 flies being allowed for every gram weight of fish. For random feeding, fish were allowed to feed for 75 minutes by which time about five-sixths of the flies had fallen into the water.

For experimental feedings in which fish were fed a number of flies all at once, an allotment of

etherized, normal winged flies, *D. virilis*, was dumped into the centers of tanks. Because of its large size, just 5 *D. virilis* were allocated for every gram weight of fish.

The objective of this experiment was to test the effects of 2 different feeding procedures on the outcome of competition. For this purpose, 2 lots of paired salmon were used. In Lot 1, 12 pairs of fish were fed at random, and then, at the end of the experimental feeding, were fed a definite concentration of flies all at once. In Lot 2, 15 pairs were fed at first a number of flies all at once, and then, were fed at random, the sequence of feeding thus being reversed.

After experimental feeding, the fish were sacrificed and the numbers of *D. virilis* and *D. melanogaster* eaten by each fish were counted in their stomachs.

Although 2 exceptions occurred in which the lighter of 2 fish about equal in weight captured more flies, the fish of a pair which contained the most flies is referred to, for convenience, as the heavier fish. The numbers of each species of fly in heavier fish were expressed as percentages of the total in both fish. The means of the percentages for Lots 1 and 2 are given in Table I.

TABLE I. A summary of the response of the heavier salmon of a pair in relation to the order in which flies at 2 levels of availability were proffered

	Arithmetic means of the percentages of flies eaten by the heavier fish of a pair	
	<i>D. melanogaster</i> proffered singly	<i>D. virilis</i> proffered all at once
Lot 1. Fish fed flies singly at random, and then, fed a number of flies all at once.....	93.80	89.22
Lot 2. Fish fed a number of flies all at once, and then, fed flies singly at random.....	92.80	76.05

For statistical treatment, the observations were considered paired and a t-test of significance was utilized. For Lot 1, there is no significant difference between the mean values of the percentage flies eaten by the dominant fish in this particular sequence of feeding. For Lot 2, the mean difference is 16.75; the standard error of the mean difference, 5.24% of flies eaten; and "t," 3.20 for 14 degrees of freedom, which is highly significant.

The difference in results can be understood if one understands that aggressive behavior inter-

feres with the feeding response and consequently, that the number of flies eaten by subordinate fish in a large measure depends on the psychological balance struck between fear of punishment and success in capturing food.

When pairs of fish were fed flies one by one, the dominant fish had an opportunity not only to defend the feeding territory, but also had time between offerings of food to chase and punish its subordinate so that the subordinate fish became conditioned not to feed. This conditioning effect continued even when numerous flies were dumped simultaneously on the water, the dominant fish now being able to guard successfully the flies as well as to eat them.

In contrast, when many flies were precipitated on the water all together at the start of feeding, food was plentiful and a feeding hierarchy was not established. Consequently, the subordinate fish was not conditioned not to feed and the dominant fish was more stimulated to eat flies than to chase and prevent its competitor from obtaining food. After the first group of flies were eaten and flies were proffered at random, the dominant fish hindered or prevented the feeding of the subordinate fish by attacking it.

EXPERIMENT II.

THE ROLE OF DOMINANCY IN FEEDING SUCCESS IN YOUNG SALMON AND BASS

Experimental design

Young-of-the-year coho salmon and young-of-the-year largemouth bass, *Micropterus salmoides* (Lacépède), were so selected that in 16 pairs of salmon and 38 pairs of bass the 2 fish in a pair were about equal in weight and in 6 pairs of salmon and 22 pairs of bass their weights were in a ratio of about 2 to 3. The salmon ranged from 1.3 to 2.8 g in weight and 51 to 64 mm in fork length; the bass, from 0.4 to 3.8 g and 35 to 69 mm. To recognize individual fish of equal size, the dorsal lobe of the caudal fin of one and the ventral lobe of the caudal fin of the other fish were clipped.

A food conditioning period of one week was used to condition fish to feeding on fruit flies, as well as to their new environment and to the presence of the observer. During this period the fish which were placed in fourteen gallon tubs ($12 \pm 1^\circ\text{C}$), were separated by clear glass partitions and fed etherized *D. melanogaster*, a daily ration of 1.0% of body weight for salmon and 1.2% for bass. At the end of the last conditioning feeding, the glass partitions were removed one day before the first experimental feeding

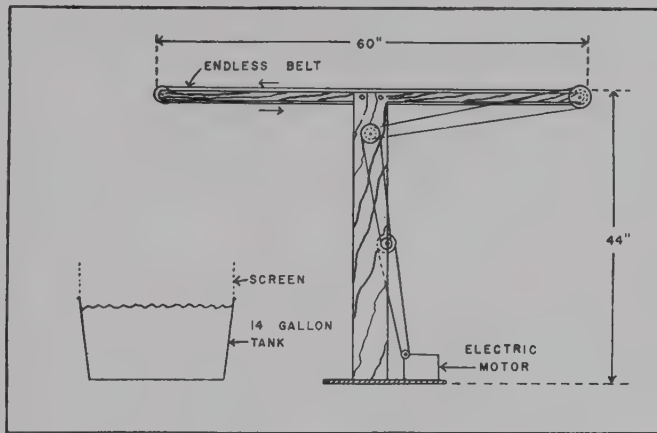


FIG. 1. A conveyor belt, feeding device used to drop etherized flies one at a time, at regular intervals, into a fish tank.

period for salmon, and about one minute before, for bass.

For experimental feedings, a total of 6,771 flies was fed to salmon, and 15,065 to bass. The salmon were fed 50 flies once a day at the rate of 4 flies per minute except for the last 2 regulated feedings when they were fed at the rate of 8 and 16 flies per minute. Bass were fed constantly at the rate of 8 flies per minute but were fed varying numbers of flies according to the size of the dominant fish. This regulated feeding was accomplished by a power driven conveyor belt type of feeding device illustrated in Figure 1 which permitted flies to be added without visible motion on the part of the observer. For final experimental feeding periods salmon and bass were fed an allotment of flies, all at one instant, and frequency and severity of aggression were recorded for bass but not for salmon.

For a short interval after each experimental feeding period, the fish were separated and the subordinate ones fed a proportionate number of flies. This was done to prevent any changes in behavior due to hunger drive. In addition, this technique enabled results to be discarded from fish no longer exposed to attack, which were not responding to food due to a factor such as sickness.

Behavior of competing fish

In bass and salmon, aggressive behavior is very similar to that in sunfish. Hoar (1951) has described aggressive behavior in coho salmon and Stringer and Hoar (1955) in Kamloops trout. In exceptional cases in this research, when dominance was being first established, both salmon

and bass locked jaws while fighting. This phenomenon has also been observed in cichlid fishes, Baerends and Baerends-Van Roon (1950), in jewel fish, Noble and Curtis (1939) and in sunfish, Greenberg (1947).

For all feedings the constant attention of the observer was required to note every change in behavior of competing fish. When fish were fed flies one at a time, the dominant fish patrolled the tank. The subordinate fish usually remained stationary at the bottom periphery of the tank. Sometimes the subordinate fish was allowed to approach the center of the tank where the flies were falling, providing it did so slowly with no quick movements. In most cases, the subordinate fish was driven back to the periphery by the dominant after a short interval. The act of feeding or even the unsuccessful attempt of the subordinate to capture a fly stimulated the dominant fish to chase it. After being chased the subordinate fish often remained quiescent for a short time at the bottom periphery of the tank. In order to capture flies, the subordinate fish had to dart repeatedly to the center of the tank and afterward suffer being chased or bitten by the dominant. When the dominant's hunger drive was satisfied, the fish would guard, or attempt to guard, flies accumulating on the surface of the water in the center area of the tanks.

Measurement of aggression

Each fly eaten by each fish was counted and numbered in sequence, and the occurrence and severity of aggression which occurred after a particular fly was eaten were noted. Frequency of aggression was established by counting the

number of feeding intervals in which aggressive acts occurred, the act of eating a fly by either fish being the criterion for delimiting acts of aggression.

A total of 446 separate aggressive acts was observed for salmon (22 pairs), 437 by the dominant and 9 by the subordinate fish, and 1,778 for bass (58 pairs), 1,653 by the dominant and 125 by the subordinate fish. The maximum frequency of aggression was 16 for salmon and 23 for bass.

A scale for weighting different acts of aggressiveness was devised as follows:

- 1—for threats such as an undulation or weaving of the body, dilation of the gills, or simply darting toward the subordinate as if to attack;
- 2—for nipping or attempting to nip without driving;
- 3—for driving without nipping or attempting to nip;
- 4—for driving and nipping or attempting to nip.

Because of difficulty in seeing whether or not a fish was actually nipped, attempts to nip were classed with actual nips. If the fish chased in spurts, drivings were counted in numbers of spurts, or if chasings were almost continuous, once around the tank was counted as a driving.

By dividing the total of all aggressive acts by the total frequency of aggression, the average severity of aggression was determined. These methods of computing frequency and severity are analogous to those used by Hall and Klein (1942) for rats. For any one feeding period, the maximum total of all aggressive acts was 52 for salmon (50 flies fed) and 144 for bass (48 flies fed), and the maximum severity of aggression was 22 for salmon and 36 for bass.

Daily trends in feeding behavior

The results indicate that the behavior pattern of the dominant fish from day to day was markedly erratic. This was attributed partly to the relatively short time of observations for each pair, and partly to a composite of psychological factors embodying the external stimuli of movement by subordinate fish and by flies falling on the surface of the water, the internal stimulus of hunger drive, and certain conditioned effects related to aggressiveness and success in feeding. In spite of this marked variability, the data showed that in many cases the changes were all in the same direction, as if a balance between dominance

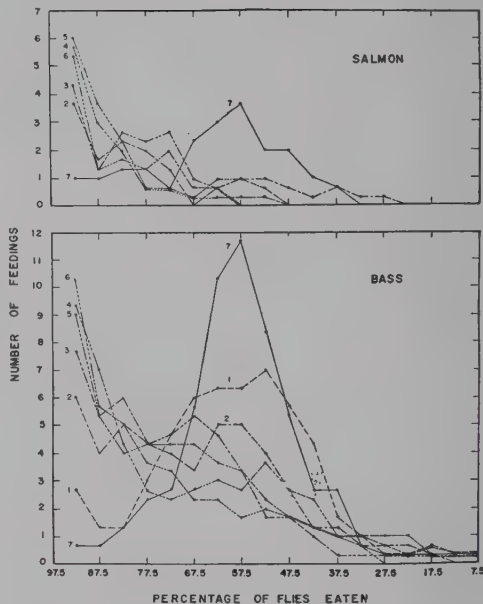


FIG. 2. The number of feedings (moving average of 3) per feeding period in which different percentages of flies were eaten by dominant fish of a pair. Each line represents a feeding period spaced one day apart. In feeding period 7, many flies were proffered all at once instead of one at a time.

and hunger drive were becoming gradually established.

To prevent extreme daily variations from hiding the general trend of behavioral changes during feedings, a moving average of 3 was adopted to smooth out the frequency distributions in Figures 2, 3, and 4.

For both salmon and bass, Figure 2 compares the number of feedings per feeding period in which the dominant fish captured flies at specific percentage levels of ingestion. The percentages of flies eaten are grouped in class intervals of 5%. For clarity, the class limits of the higher 3 intervals are 85.1-90.0, 90.1-95.0, and 95.1-100.0%; the corresponding class marks are 87.5, 92.5, and 97.5%.

Experimental feeding periods were spaced one day apart and are represented by incomplete frequency polygons which are numbered consecutively, 1-7 for bass and 2-7 for salmon. Each frequency polygon represents a total of 58 feedings in bass and, in salmon, a total of 22 feedings. The polygon of feeding period 1, for salmon, is not given because 16 out of 22 pairs of fish failed to respond to food.

Lack of physical contact between bass before the first experimental feeding period resulted in an approximately normal distribution for the first feeding period. That the mode and median are higher than the 50% mark is probably partly due to a certain amount of visual intimidation through the clear glass partitions such as dilation of the gills, energetically pushing against the partitions, and threatening, weaving movements of the body mentioned earlier.

In successive feeding periods 2 to 6, the frequency polygons exhibit marked positive skewness for salmon and bass. Values of the frequency of feeding at the 92.5% mark increase progressively with successive feeding periods except for the 6th for salmon and the 5th for bass being out of sequence. This orderly increase reflects a trend in which more fish exhibit greater feeding dominance each successive day.

For feeding period 7, a group of flies was dumped on the water all at once. This change in feeding method almost eliminated the feeding hierarchy in most pairs. For both species of fish, the modes of feeding period 7 were at the

57.5% mark for flies captured. That this value is about 7.5% more than might be expected if all conditions were equal is attributed partly to the conditioning effect of previous aggression causing a lag in the response of the subordinate to feeding. That aggression is subservient to hunger drive is indicated by the almost complete cessation of driving when fish were fed numerous flies at one time. Figures 3 and 4 show that for bass some aggressive action did occur which was mostly confined, however, to the end of feeding period 7 when but a few flies remained on the water and thus, could not greatly influence the percentage of flies captured.

Complete feeding dominance in which the dominant fish captured all the flies was exhibited in 5, 8, 6, 6, 7 and 2 cases out of 22 for salmon in feeding periods 2 to 7, respectively, and in 5, 11, 9, 10, 9, 12 and 2 cases out of 58 for bass in feeding periods 1 to 7, respectively.

Daily trends in aggressive behavior

For bass, Figure 3 shows the number of feedings per feeding period in which driving and

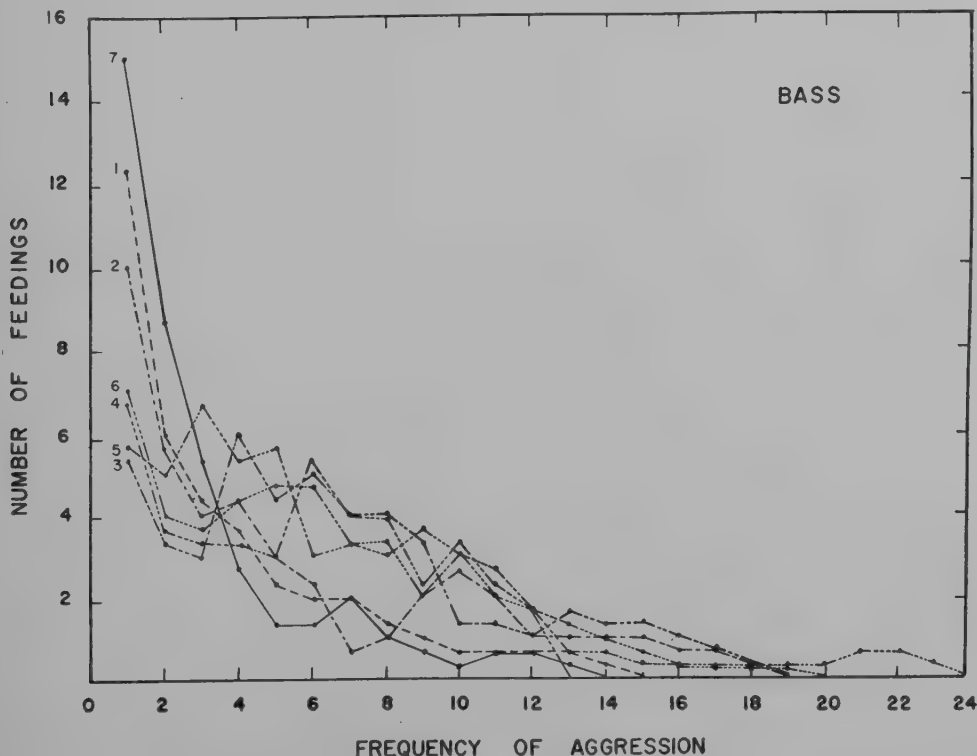


FIG. 3. The number of feedings (moving average of 3) per feeding period in which specific counts of aggressive acts such as driving occurred. Each line represents a feeding period spaced one day apart. In feeding period 7, many flies were proffered all at once instead of one at a time.

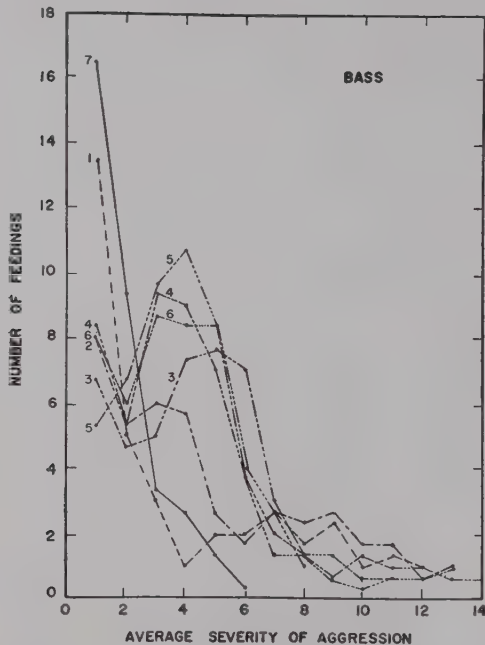


FIG. 4. The number of feedings (moving of 3) per feeding period in which specific levels of severity of aggression were measured. Each line represents a feeding period spaced one day apart. In feeding period 7, many flies were proffered all at once instead of one at a time.

other aggressive acts occurred at various frequencies.

The amount the subordinate stimulates the dominant to chase is determined partly by previous conditioning. The average frequency of driving was quite low for bass when the feeding period occurred immediately after the removal of the glass partitions, allowing physical contact between bass for the first time. More chasing occurred in feeding periods 2 to 6. In feeding period 7, when bass were fed many flies at once, the frequency distribution for aggression returned to the curved pattern of the first period, the presence of many flies on the surface of the water stimulating the dominant fish to feed rather than to chase.

Although not graphed for salmon, the pattern of the frequency of aggression in feeding periods 2 to 6 was similar to that for bass. Aggression in salmon was not recorded for feeding periods 1 and 7.

No chasing occurred in 3, 2, 4, 3 and 7 cases out of 22 for salmon in feeding periods 2 to 6, and 22, 11, 12, 10, 5, 8 and 23 cases out of 58 for bass in periods 1 to 7.

For bass, Figure 4 shows the number of feedings per feeding period in which aggressive acts occurred at different average intensities. The frequency distribution of the severity of aggression in the first and 7th feeding periods is markedly positively skewed. Such skewness is due to a lack of physical contact between pairs before the first feeding period and to an abundance of flies on the water, which inhibited chasing, during the 7th period. In feeding periods 2 to 6 a mode develops about an average intensity of 4.

Although not illustrated for salmon, feeding periods 2 to 6 are compactly grouped and exhibit a negative and approximately straight line relationship.

Frequency of aggression versus feeding success

The Chi-square test of significance at the 5% level of probability was used as a statistical tool for separating random variation from variation caused by other factors influencing the response of fish to eating flies. Because some pairs of fish took longer than others to reach an equilibrium in their feeding level, only the last 3 feeding periods in which fish were fed flies one at a time were evaluated. No significant heterogeneity was

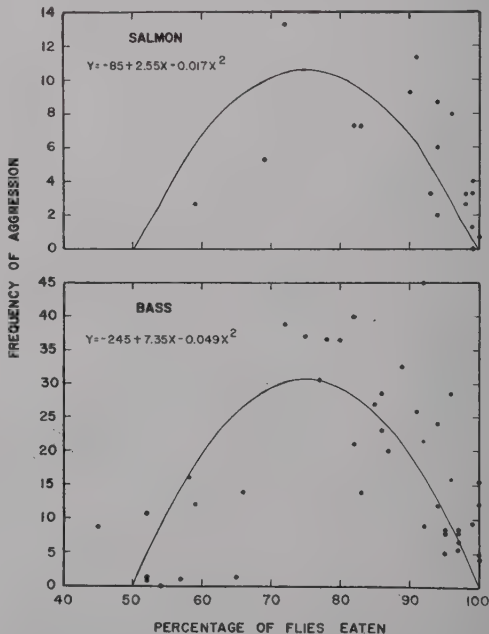


FIG. 5. The relationship between the frequency of aggressive acts by dominant fish per 100 flies eaten and the percentage of flies eaten when fish were fed flies one at a time.

found in the percentage of flies eaten for 19 out of 22 pairs of salmon and 43 out of 58 pairs of bass.

The relationship between frequency of aggression per 100 flies and number of flies captured by the dominant fish expressed as a percentage is indicated in Figure 5. Because the presence of a fly on the water stimulated the subordinate fish to feed, and this, in turn, stimulated the dominant fish to chase, the frequency of aggression was chosen as the dependent and the percentage flies eaten as the independent variable.

Casual inspection of the 2 graphs gives the impression of little trend, but study and reasoning along biological lines based on the detailed observation of the behavior of the fish suggests that the relationship is best expressed by a curve with a maximum in the dependent variable. For simplicity, a parabola which on theoretical grounds was restricted to pass through the (50.0) and (0.0) points was selected as the curve to fit to the data. Minimum driving occurs at the 100% level because the subordinate is subdued or if not subdued is subjected to a high severity of attack and thus the dominant fish captures almost all of the flies with the minimum amount of chasing. In contrast, at the 50% level, little chasing occurs because dominance if present is weak and both fish have almost equal opportunities to feed.

Indices of correlation calculated for the parabolas in Figure 5 are 0.588 for salmon and 0.547 for bass, both being highly significant.

Index of dominance

Because of the parabolic nature of aggressive activity in Figure 5, no linear regression existed between measurable body characteristics such as weight and frequency of aggression. For this reason, and because the level of aggression and numbers of flies eaten varied from day to day in most pairs, a scale was devised which weighted different degrees of dominance as follows:

- 0—when dominance was reversed (the usual subordinate becoming dominant).
- 1—when the ratio of chasing by the dominant to flies eaten by the subordinate was low ($1/2$ or less).
- 2—when the ratio of chasing by the dominant to flies eaten by the subordinate was about equal ($1/2$ to $2/1$).
- 3—when the ratio of chasing by the dominant to flies eaten by the subordinate was high ($2/1$ or more).
- 4—when the subordinate was conditioned not to feed (no chasing by the dominant and few flies eaten by the subordinate).

An index of dominance was obtained by totalling the scale values obtained each day for feeding periods 1 to 6. Ratios and scale values were arbitrarily selected but order of selection was based on theoretical considerations. A low ratio of chasing to flies eaten indicates a low level of dominance in that the dominant fish was not responding every time to the stimulus of the subordinate capturing a fly. A high ratio suggests a high level of dominance in that the subordinate was punished more than it was rewarded. This index permitted the use of all the data including periods in which dominance was reversed and in which the subordinate was conditioned not to feed. Many subordinate fish were in such a state of subjection that they made little or no attempt to capture flies during feeding periods and, consequently, the dominant fish did not have to chase them. The dominant fish presumably had chased the subordinate so severely between feeding periods that the subordinate was conditioned not to feed.

Variations in aggressive activity and feeding success could be partly due to the subordinate learning to avoid punishment. Such learning is probably closely associated with conditioning between and during feeding periods.

The possibility exists that the subordinate fish learned to wait until the glass partitions were in place and they were fed unmolested a proportionate share of flies to compensate for what they did not get while in forced association with the dominant fish. This procedure was used to minimize any difference in hunger drive between competing fish. Analyses of the data for individual pairs of bass on the basis of the feeding stability found in feeding periods 4 to 6 suggested that learning to wait was not an important factor in this experiment. That the subordinate bass on the average obtained about 23% more flies in feeding period 7 than in feeding period 6 also supports this supposition.

Discussion

The attempt in this experiment was to isolate and study certain measurable features basic to success in competition, and evaluate their importance. The 4 factors tested which could influence the frequency and severity of aggression were the mean K_n , the percentage K_n , the mean weight, and the percentage weight of the pair of competing fish. Correlations which were significant for these factors are noted in Table II. With one exception for salmon and one for bass, no significant direct relationship between the 4 factors and percentage of flies eaten could be dem-

TABLE II. Summary of correlations for 22 pairs of salmon and 58 pairs of bass fed flies singly at regular intervals for 6 feeding periods. (D is an index of dominance; F is the percentage of flies eaten by the dominant fish; M is the mean weight of the pair; S is the severity of aggression by the dominant fish; and W is the percentage weight of the dominant fish)

Fish	Correlations	Correlation coefficient	Probability
Salmon.....	r_{MF}	0.463	0.05
	r_{MD}	0.568	0.01
	r_{DF}	0.668	0.01
	r_{MS}	0.634	0.01
Bass.....	r_{WF}	0.523	0.01
	r_{WD}	0.535	0.01
	r_{DF}	0.875	0.01

onstrated. Certain factors, however, are shown to be indirectly related through the medium of aggression.

Because factors governing competition must be expressed through the dynamic medium of aggression, there is little chance of obtaining high direct correlations between these factors and percentage flies eaten. Consequently, correlation coefficients between a factor such as percentage weight and percentage flies eaten cannot be expected to be high in a narrow weight range. Only by increasing the weight range as was done in experiments described later can significant relations be established.

EXPERIMENT III.

INTRASPECIFIC COMPETITION IN YOUNG SUNFISH AND BASS GROUPED IN PAIRS

Experimental design

Fifty-four pairs of young-of-the-year largemouth bass in 8 separate lots, and 51 pairs of pumpkinseed sunfish, *Lepomis gibbosus* (Linnaeus), in 6 lots, were matched in competition for live flies which could be captured at irregular intervals. Except for 9 sunfish in their 2nd summer that were matched with young-of-the-year fish in order to obtain extreme size differences, all the sunfish used in this experiment were young-of-the-year.

A battery of 10 glass aquaria, suitably aerated and containing about 12 liters of water, was used for all of the bass and about two-thirds of the sunfish. For the remaining sunfish a battery of

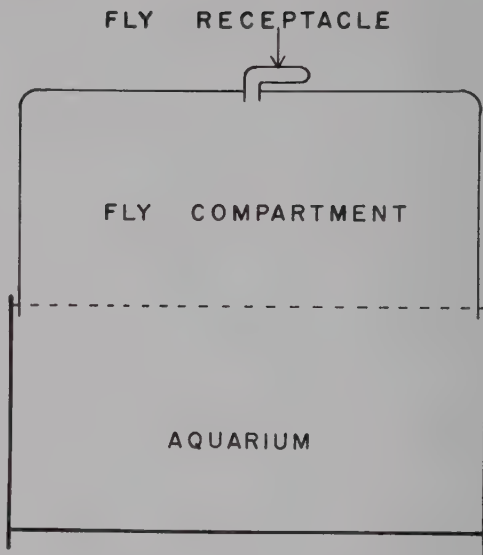


FIG. 6. A diagram illustrating the relative size and position of a plastic fly compartment and glass fly receptacle in which etherized fruit flies were placed prior to regaining activity. The dotted line represents the surface of the water.

10 clear glass, one-gallon bottles, each one containing about 3 liters of water, was provided. Water temperatures were $22 \pm 2^\circ\text{C}$ and varied among lots.

For irregular or random feeding, plastic (Figure 6) or glass compartments confined live flies over the surface of water. Flies were etherized for ease of counting and handling and were placed in special receptacles which gave access to the compartments. These receptacles enabled almost all the flies to recover fully from the effects of ether and to enter the compartments and distribute themselves at random. Occasionally, however, a fly might fall on the water before it had regained full control of its faculties. Practically no flies were captured while flying, but were captured when they alighted on the water or when they crawled down the sides of a compartment close to the water.

Except for 3 lots which were given conditional feedings, the bass, on capture, were deprived of food until the experimental feedings. Sunfish were conditioned to feeding on fruit flies for one or 2 days and, before experimental feedings, were deprived of food for one day. Pairs that contained fish in their 2nd summer were fed *D. virilis* and those, in their first summer were fed *D. melanogaster*. The number of flies available to both competing fish had to be few enough

that neither fish could sate its appetite nor completely fill its stomach. Experimental feedings were run simultaneously for 2-hour periods for all pairs of fish in a lot, after which the fish were sacrificed and flies counted in the stomach.

Behavior of competing sunfish

Aggressive behavior in green sunfish (*Lepomis cyanellus*) has been adequately described by Greenberg (1947). No qualitative differences were discernible between that described for green sunfish and that observed for the pumpkinseed sunfish used in this work. Driving was common throughout the experiments. A defense posture, however, was often used. Upon being chased, a subordinate fish would often seek respite by placing its abdomen in a corner of the side and bottom of an aquarium and tilt its body in such a position that its dorsal spines when erect would point towards its attackers. In some pairs, the subordinate fish when severely chased would retreat to a corner at the surface. For feeding purposes, a fish at the surface would be seriously handicapped because its area of vision would be very restricted. In extreme cases of subjugation, a subordinate fish would place its head in a corner, a position still further restricting its vision and practically prohibiting feeding. In contrast, a dominant fish had free reign of territory and was unrestricted in its search for food.

Weight versus feeding success

The relation between percentage weight and percentage of flies eaten are depicted graphically in Figure 7 for bass and sunfish.

While no precise mathematical interpretation is intended, sigmoid curves were used to represent the trend of the values. Solid points and a solid line represent the heavier fish. When weights are equal a curve representing these values would be expected to pass, theoretically, through the (50,50) point. The curve approaches the upper limit asymptotically.

Exponential curves of the type, $F = Be^{kw}$, for lighter fish and, $F = A - Be^{-k(w-w^*)}$, for heavier fish suitably describe the trend. In these equations, F stands for percentage of flies eaten; w , percentage weight; w^* , 50% weight; B , a parameter; A , the maximum degree of success, i.e. 100% flies eaten; e , base of natural logarithms; and k , the instantaneous rate in terms of percentage flies eaten. The equations were derived by graphical methods explained by Brody (1945).

The pattern of scatter of points is about the same for both graphs, scatter being less at the higher weight levels and greatest where weights are about equal. As weight differences decrease other factors determining the outcome of competition increase in importance causing this scatter. Four cases arose in which lighter sunfish won

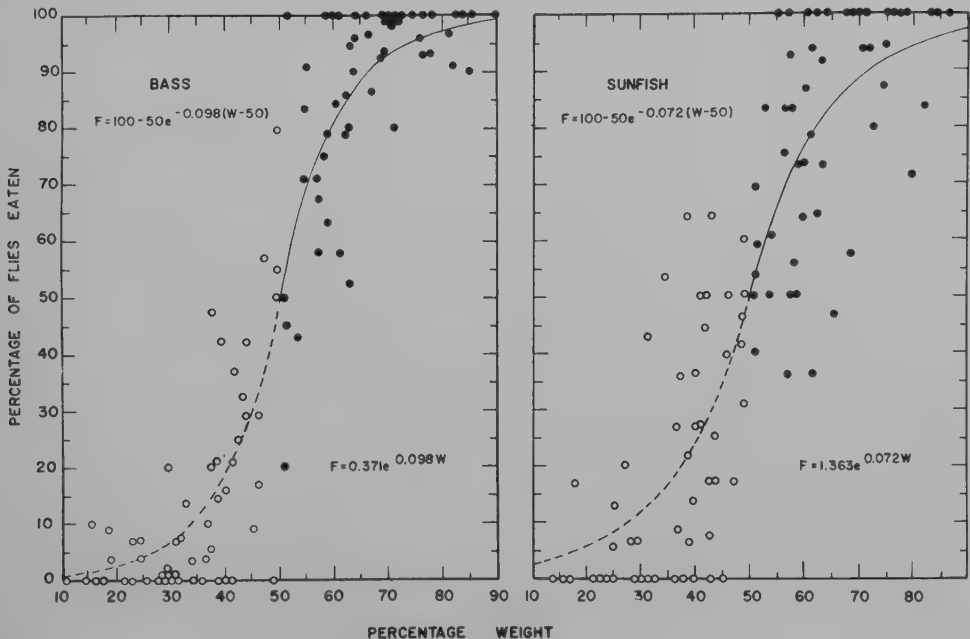


FIG. 7. Graphs of fish in pairs competing for flies proffered at random. (Solid points represent heavier fish, hollow points, lighter fish in a pair).

out in competition for flies indicating that weight does not always govern the outcome of competition. Although differences in the shape of the 2 curves are probably not significant, the scatter is smaller for bass. This might be partly due to more uniform experimental conditions and to shorter periods of captivity for bass.

Although curvilinear correlations would have increased significance, simple linear statistics were used for purposes of analysis. The simpler procedure was chosen partly because of the large scatter of individual points; partly because of the uncertain nature of the regression curve; and partly because of the doubtful advantage of calculating an index of correlation instead of a correlation coefficient when the curvature of the regression curve was not very marked over the range of values obtained.

For most purposes each pair is considered the unit; consequently, for purposes of computation of significance, only half the number of points for individuals are used.

TABLE III. Summary of correlations for 51 pairs of immature sunfish and 54 pairs of young-of-the-year bass fed flies at random for one feeding period. (W is the percentage weight; F is the percentage of flies eaten; and K is the relative condition coefficient)

Fish	Correlations	DOMINANT FISH		HEAVIER FISH	
		Correlation coefficient	Probability	Correlation coefficient	Probability
Sunfish	r_{WF}	0.643	0.01	0.534	0.01
	r_{KF}	0.309	0.05	0.300	0.05
	$r_{F,WK}$	0.698	0.01	0.598	0.01
Bass	r_{WF}	0.618	0.01	0.621	0.01

Correlation coefficients are given in Table III for the relation between percentage weight and percentage of flies eaten for the points shown in Fig. 7. In earlier experiments, because the dominant fish almost always were observed to capture the most flies even though reversals in dominance sometimes occurred, fish which ate more than 50% of the flies in this experiment were assumed to be dominant.

*Relative condition coefficient
versus feeding success*

Length of time of captivity (an average of 32 days) altered the condition or plumpness of sunfish more than would normally occur in summer in nature. This was probably due to internal

hierarchical pressure in the laboratory favoring the more dominant individuals in capturing food.

As indicated by the values of the correlation coefficients in Table III, the K_n contributed significantly to the feeding success of sunfish under laboratory conditions. Because factors other than weight could be expected to cause greater variation in percentage of flies eaten in the middle of the weight range than at the extremities, the data were arbitrarily divided into thirds and the relation of the K_n to the percentage of flies eaten by the middle two-thirds was tested (weight range, 50.6-68.5% for larger fish, and 34.5-68.5% for dominant fish). For heavier fish, $r = 0.456$ and for dominant fish, $r = 0.425$ both correlations being highly significant with P-values of less than 1%.

In contrast, the correlation coefficient, $r = 0.004$ for the extreme third of the sunfish (weight range, 68.6-86.4%) was not significant. This means that the K_n had no detectable effect as a factor influencing competition when differences in weight were great.

A multiple correlation representing the combined effects of percentage weight and percentage K_n as would be expected, gave the highest correlations.

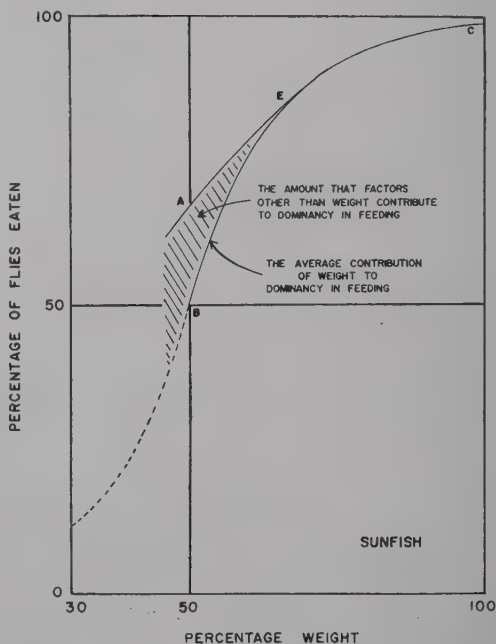


FIG. 8. A comparison of 2 curves representing the percentage of flies eaten by sunfish in Figure 7 selected on the basis of dominance (line AEC) and those eaten by sunfish selected on the basis of weight (line BEC).

The bass used in this experiment were held captive an average of only 6.4 days and, consequently, there was no significant correlation between the K_n and feeding success because variations in K_n were minor.

Discussion

For the sake of contrast with the sigmoid curve BC for heavier sunfish, a curve AC representing the dominant sunfish in the upper half of Figure 7 is rather arbitrarily fitted in Figure 8. The line BC is fitted to the heavier fish of a pair and AC, the dominant fish. The average degree to which dominance in terms of percentage of flies eaten is modified by weight is indicated by the line AC. The line BC indicates that usually the heavier fish are also the dominant ones. When fish are of equal weight, dominance is still exhibited, but obviously as the percentage weight of the larger fish increases, the average percentage of flies eaten by the dominant increases. Since the percentage of flies eaten depends on the degree of dominance existing, an increase in weight causes an increase in dominance. The cross hatched area illustrates the proportion other factors contributed to dominance independently of weight.

The distance AB represents the average effect of unmeasured factors that have contributed to dominance when the weights of matched fish are equal. As the percentage weight of the dominant fish becomes smaller, factors like that measured by the K_n must play an increasingly important part for the fish to remain dominant. As the percentage weight of the dominant fish increases, other factors contributing to dominance become of lesser importance. Finally at point E where lines AC and BC merge, other factors besides weight contributing to dominance are practically of no importance. The possibility of reversals in dominance exists below point E. The smaller the percentage weights of the dominant fish, the greater are the chances of a reversal occurring. Thus, the less the percentage weight of the dominant fish, the less stable a hierarchy is likely to exist.

EXPERIMENT IV.

COMPETITION BETWEEN OLDER SUNFISH GROUPED IN PAIRS

One lot of 32 pairs of sunfish, aged 1 to 5 years, was used in this experiment. The fish were sorted into 3 size groups in which the larger fish formed roughly 55, 65, and 75% of the weight of the pair. Pairs were placed in black wooden troughs during conditioning periods. Individuals of the pair were separated by clear glass partitions, permit-

ting them to see each other but not make physical contact.

As in the previous experiment, flies were confined in transparent compartments over the water. For conditioning feedings, fish were fed an equivalent of 2% of their body weight on the 4th, 6th, and 8th day of captivity. The partitions were removed just prior to experimental feedings. On the 10th day (water temperature, 19.5°C), fish were allocated 3 flies per gram weight of fish, after which they were sacrificed and stomach contents counted.

Although 32 pairs of sunfish were originally set up for analysis, only 20 pairs ate sufficient flies for an adequate test of competition. This was attributed, partly, to low air temperature which limited the activity of the flies making them unavailable for capture. As a result, data from pairs of fish which captured less than one-fifth of the flies offered or ate less than 8 flies where the number of flies offered was small were deleted from the results. Examination of the discarded data showed that the conclusions are not biased by the omissions.

Because older sunfish were utilized in this experiment, information with regard to age, sex and effect of parasitism by a tapeworm, *Glaridacris* sp., was obtained. The ages of the sunfish were determined by scale reading and percentage age was calculated in the same manner as percentage weight. Since only 12 of the 20 pairs were parasitized by *Glaridacris*, a method analogous to the treatment of other data was not possible and degree of parasitism was expressed as a difference in percentage body weight parasitized.

Table IV compares correlations for sunfish grouped on the basis of dominance and on the basis of weight.

Because of the smaller number of pairs involved in this experiment, the significance of results for percentage weight values was lower than that found for young-of-the-year sunfish in Experiment III. That heavier fish give a different correlation value from that of dominant fish is due to 2 heavier fish in the same age class being subordinate instead of dominant. The data from these 2 fish increased the range of values for percentage of flies eaten at the 50% weight point for heavier fish and decreased the range for dominant fish. Thus, a higher correlation coefficient for heavier fish was obtained.

The correlations between percentage of flies eaten and percentage K_n are not significant by themselves. The fact that the K_n was of less significance for older fish than young-of-the-year

TABLE IV. Summary of correlations for 20 pairs of sunfish of various ages fed flies at random for one feeding period. (W is the percentage weight; F is the percentage of flies eaten; K is the relative condition coefficient; and A is percentage age. Where probabilities are not stated, the correlations are not significantly different from zero at the 5% level)

Correlations	DOMINANT FISH		HEAVIER FISH	
	Correlation coefficient	Probability	Correlation coefficient	Probability
r_{WF}	0.521	0.05	0.546	0.02
r_{KF}	0.179	—	0.297	—
$r_{F,WK}$	0.587	0.05	0.591	0.05
r_{AF}	0.668	0.01	0.726	0.01

sunfish was partly due to the uniformity of their conditioning. The coefficients for multiple correlations for both dominant and heavier fish are significant, and measure the success of estimating percentage of flies eaten from percentage weight and percentage K_n data.

Although older sunfish have been subject to many more intraspecific encounters than young-of-the-year sunfish, the relation of percentage weight and of flies eaten in competition by the former is very similar to that of the latter.

Because a complex of intrinsic factors in addition to size contribute to longevity, one might expect age to be more significant than weight as a criterion for judging the outcome of competition. That this is the case is indicated by the much higher correlations obtained for percentage age than for percentage weight.

The relationship between parasitism and percentage flies eaten was tested for dominant fish and was found not significant.

The role of sex was obscure because of the small number of fish used. Out of 11 heterosexual pairs, the males were dominant 6 times and the females 5 times.

EXPERIMENT V.

COMPETITION AMONG YOUNG SUNFISH GROUPED IN TRIOS

Thirty-five groups of 3 sunfish were placed in one-gallon, clear glass bottles—21 on the 4th and 14 on the 6th day of captivity. The bottles were filled $\frac{3}{4}$ full of water and during the experimental feeding water temperature was 29°C. All groups were given a conditioning feeding of 40 flies apiece on the 6th day and the fish were allowed to feed on them for 2 days. At the end of this period, the

remaining flies were allowed to escape and the fish were starved for 2 days.

On the 10th day of captivity, 20 etherized *D. melanogaster* were placed in fly receptacles which permitted the flies access to the upper third of the jar where they could be captured by fish. After 2 hours of feeding the fish were sacrificed and flies counted in their stomachs.

Figure 9 shows the distribution of values for all 3 matched fish. Theoretically, a regression line representing percentage flies eaten plotted against percentage weight would pass through the (33.3, 33.3) point of the graph. Assuming that 3 fish are of equal size, that other conditions are equal, and that no dominance exists, one would expect each fish to eat an equal number of flies. In spite of the considerable scatter, a calculated regression line does pass through this point.

The correlation for the effect of percentage weight on percentage of flies eaten was 0.678, the P-value being less than 0.01.

In this experiment, hierarchical relationships were not recorded either before or during experimental feeding. Consequently, the status of individuals could not be established and fish were not separated on the basis of rank order.

GENERAL DISCUSSION

Theoretical implications and practical significance resulting from this investigation may

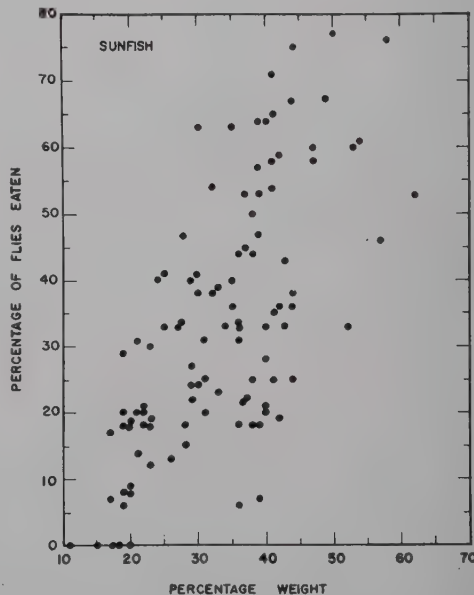


FIG. 9. The relationship between percentage of flies eaten and percentage weight of sunfish competing in trios.

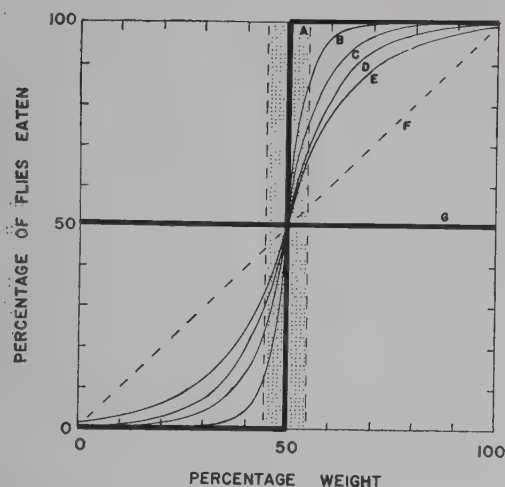


FIG. 10. A graph showing theoretical limits of the partitioning effect of weight on flies eaten in intraspecific competition in fish competing in pairs. (The line A represents the maximum degree and the line G, the minimum degree of competition obtainable. The broken line, F, represents flies partitioned in direct proportion to weight. The exponential curves, B, C, D, and E represent data found by experiment).

best be explained by reference to Figure 10. This figure represents the effect of a factor such as weight contributing to success in competition between 2 fish. The dotted area indicates a zone in which a chance distribution of factors other than percentage weight may cause reversals in dominance and in which the heavier fish may not necessarily be the dominant one. The heavy line, A, represents the maximum average effect of weight on flies eaten. This is an extreme situation in which fish possessing other qualities which favor success need only a slight advantage in weight to completely exclude its competitor from a food supply. In this investigation, such a situation was most closely approached with salmon and bass that were fed flies one at a time and is described by the exponential curves B and C which are fitted to the data. When flies were fed at random, competition was less extreme, the flies being less localized and occasionally 2 or more flies being available for capture in different areas at the same instant. The exponential curves D and E represent this situation for bass and sunfish respectively. The diagonal, broken line, F, describes a situation in which the amount of food obtained is directly proportional to the weight of the competing fish. Such a situation is not likely to occur among fish exhibiting feeding dominance except when the food supply is overly abundant, where fish are isolated by natural bar-

riers or have sufficient space to make competition impossible. The heavy horizontal line, G, represents a situation where there is virtually no competition between fish either because of lack of dominance or because food is so thinly dispersed that fish would have to search independently for it. This last possibility could result in stunted populations since the chances of finding food would be the same for large and small fish. Theoretically, if one excluded variations in metabolism, competition resulting in values lying between F and G would result in faster growth for smaller, and slower growth for larger fish, and this eventually would result in stunted populations by increasing the survival of young fish. Such a situation would partially account for stunted fish populations like those described by Alm (1946). On the other hand, values lying between A and F would favor larger fish, the larger fish obtaining greater and greater amounts of the available food supply at the expense of and consequent extermination of the smaller ones.

In Fig. 10 the difference in slope between the exponential curves C and D for bass was attributed to the techniques of feeding flies one at a time and at random, but the difference in slopes between curves B and C and between curves D and E are due to specific differences in aggressive behavior. For example, Fig. 5 shows that less chasing prevailed in salmon than in bass relative to the percentage flies captured. Consequently, for the temperatures at which the experiments were conducted, the intensity of intraspecific competition is rated in the following order: salmon first, bass second, and sunfish last.

When many flies are available at one time, a greater proportion are eaten by dominant salmon than by dominant bass which indicates that the inhibiting effect of salmon is greater than that of bass even in a less intense competitive situation. Moreover, during periods of observations, a salmon chased a competitor and captured flies noticeably faster than a bass. In future work, direct comparisons of various species of fish in competition and at different temperatures, for a direct evaluation of specific differences would be meaningful.

This research suggests that strong intraspecific competition in which physical violence is manifested by fighting, biting, and chasing results in a disproportionate partitioning of food according to weight and that this would result in ever increasing size differences within the group. In addition the effectiveness of weight in the partitioning of flies is less for sunfish in trios than in pairs; thus, the smaller the group, the more in-

tense the intraspecific competition. Finally, strong intraspecific competition does not occur when food is overly abundant as indicated by the marked decrease in chasing when a lot of flies are fed fish at one time. Difficulties presented by Langlois (1936) connected with keeping bass stocks sufficiently uniform in size to prevent cannibalism are partially explained by the effects of competition for food particles resulting in ever increasing size differences, competition ending when predation began.

In conclusion, it may be emphasized that this research in many respects foreshadows many problems, being but a prelude to future investigations.

SUMMARY AND CONCLUSIONS

1. This paper presents a series of experimental situations designed to test, quantitatively, the impact of aggressive behavior and other measurable characters on the feeding success of fish in intraspecific competition for a limited food supply. Three species of fish were utilized and, unless otherwise stated below, just 2 fish were matched.

2. When salmon were proffered fruit flies in a mass, success in capturing flies depended on whether or not flies were offered singly ahead of time. If an abundance of flies was preceded by a scarcity of flies, there was no significant difference in feeding success, but if the order was reversed, a highly significant difference between the 2 methods of feeding was obtained.

3. Up to the 3rd day, average trends in the daily feeding behavior of dominant bass fed flies singly were marked by an increase in aggressive acts and feeding success, after which the behavior pattern remained relatively stable. On the 7th day, a lot of flies made available at one time greatly reduced the aggressiveness and feeding success of the dominant fish.

4. A parabola suitably describes the relationship between frequency of aggression and percentage flies eaten by dominant salmon and bass for all degrees of aggression and, for those fish in which feeding success had become stable, indices of correlation were highly significant. The parabola describes 2 extreme behavioral situations: one, in which the subordinate is not attacked because no dominance exists and, excluding random variations, obtains half the food; the other, in which the subordinate is not attacked because it has become conditioned by previous punishment not to respond to food.

5. In salmon fed flies singly at regular intervals, positive correlations were obtained for mean

weight and severity of chasing, percentage of flies eaten, and an index of dominance, and for the index of dominance and percentage of flies eaten.

6. In bass fed flies singly at regular intervals, positive correlations were obtained for percentage weight and percentage of flies eaten, for percentage weight and an index of dominance, and for an index of dominance and percentage of flies eaten.

7. For random feeding in bass and sunfish, positive correlations were obtained between weight and percentage of flies eaten. Sigmoid curves describe the relationship. In sunfish, a positive correlation was found between percentage relative condition coefficient and percentage of flies eaten which in one experiment was attributed to a long laboratory history altering their condition.

8. Except for sunfish which were subjected to long periods of captivity, fish which were both lighter and dominant and fish which exhibited reverse dominance were restricted to a narrow range in which fish in pairs were nearly equal in weight.

9. In sunfish, a high correlation was obtained between age and success in feeding.

10. The effect of weight on percentage of flies eaten for sunfish grouped in trios was highly significant.

11. In sunfish, the degree of success in competition for flies is greater for heavier fish grouped in pairs than for the heaviest fish grouped in trios.

12. Segregation of driving into component parts, i.e., frequency and severity, has enabled a more precise interpretation of aggression. The techniques contributed by this research make possible comparative studies of factors governing interspecific and intraspecific competition under controlled conditions.

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THE DISTRIBUTION OF THE RED-BACKED SALAMANDER, *PLETHODON C. CINEREUS*, WITHIN THE SOIL¹

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INTRODUCTION

Salamanders have been the subjects of many ecological studies but little is known of their population ecology. It has been estimated by Conant (1952) that they are among the most abundant terrestrial animals, yet they, and any effects which they may have on their environment, are often ignored.

The purpose of this work has been to study the distribution of *Plethodon c. cinereus* within the soil as a means of interpreting field captures. Most field studies of salamanders have been based upon captures made beneath superficial shelter objects such as logs and stones, although it has been known that the salamanders thus captured might not constitute a major part of the population (Test and Bingham 1948). Seasonal differ-

ences in the surface captures may reflect differences in the behavior of individuals rather than changes in the population as by death or dispersal (Test 1955). While the mineral soil has been frequently suggested as a refuge (Conant 1952, Test and Bingham 1948, Vernberg 1953), it has not been adequately studied as a habitat. An understanding of the vertical distribution within the soil and the factors which influence this distribution is needed to interpret the surface captures. This study was intended as one step toward the prediction of the parameters of a population when the parameters of the surface population and the appropriate environmental factors are measured.

Three approaches were used: (1) a field plot in which a study of the surface captures of *Plethodon* was made under natural conditions, (2) underground cages, in which the vertical distribution could be measured under partially natural conditions, and (3) mazes, in which the

¹ A portion of a doctoral thesis submitted to Rutgers University.

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vertical distribution could be measured under controlled, simulated soil conditions.

METHODS

The animal

The red-backed salamander, *Plethodon c. cinereus*, is common in the northeastern part of the United States. The natural history of the lungless family Plethodontidae has been summarized by Dunn (1926). In this species the entire life cycle is completed on land. Breeding takes place during the summer, and the eggs are laid in crannies in logs; the female, and occasionally also the male, remain with the eggs. At hatching, during late summer or autumn, the young have lost their gills and are adapted for the terrestrial habitat (Noble 1954). The species feeds upon small invertebrates, primarily insects (Jamson 1944).

Location

The field studies were done in the William L. Hutcheson Memorial Forest, formerly known as Mettler's Woods, located on the eastern edge of East Millstone, Somerset County, New Jersey. The plot and underground cage studies were done in a portion of the woods which has never been cleared. The woods is the least disturbed forest stand on the piedmont plain in New Jersey.

The canopy over most of the forest consists of white oak (*Quercus alba*), black oak (*Q. velutina*), and red oak (*Q. rubra*), along with some red hickory (*Carya ovalis*), and shagbark hickory (*C. ovata*). White ash (*Fraxinus americana*), beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), Norway maple (*A. platanoides*), and sweet cherry (*Prunus avium*) contribute to the discontinuous subcanopy between the canopy and the understory. The understory layer consists of a continuous cover of flowering dogwood (*Cornus florida*). The shrub cover is markedly influenced by drainage. On the well-drained areas (ca. 50% of the plot) maple-leaved viburnum (*Viburnum acerifolium*) is the principal shrubs; the herb stratum is composed of May apple (*Podophyllum peltatum*), spring beauty (*Claytonia virginica*), rueanemone (*Anemone thalictroides*), spring cleavers (*Galium aparine*), false Solomon's seal (*Smilacina racemosa*), Solomon's seal (*Polygonatum biflorum*), jack-in-the-pulpit (*Arisaema triphyllum*), *Carex* spp., and enchanter's nightshade (*Circaea quadrifida*). The moss stratum is poorly developed. The poorly-drained area along the stream has a shrub stratum of spicebush (*Lindera benzoin*) and arrow-wood (*Viburnum dentatum*). This area differs from the main body of the forest by

the absence of a definable understory tree stratum and by the sparseness of the canopy due to the greater concentration of blown-down trees. Several species of *Rubus*, greenbrier (*Smilax rotundifolia*), and numerous saplings occur here. Herbs are abundant. Skunk-cabbage (*Symplocarpus foetidus*), spotted touch-me-not (*Impatiens capensis*), and clearweed (*Pilea pumila*) are characteristic (Monk 1957).

The soil is classified in the Penn series and is weathered from a red shale (Brunswick formation) of Triassic origin (Balloni 1958). One profile was described from an upland, well drained area as follows: A₀₀ 1 in., leaf litter of deciduous trees; A₀ 1 in., partially decomposed plant residues, very friable; A₁ 2 in., dark gray, not continuous, rather erratic, rich in organic matter; A₂ 8 in., brown, silt loam, worm holes (and mammal burrows) and roots abundant; A₃ 2 in., transition zone, no abrupt change in the horizons; B₁ 8 in., reddish yellow, silt loam; B₂ or B-D 4 in., yellowish-red, loam; C or D, at 24 in., red, sandy loam, bedrock. The soil of the stream flood plain, and in particular at the location of the underground cages, has a different nature. The A₀₀ and A₀ are thinner, the soil is very poorly drained and genetic profile development is lacking. The soil is dark gray to a depth of 10 in. where a 2 in. stone-like porous layer of clay and iron is present due to the interaction of the shifting water table and the iron from the red shale bedrock. Beneath this layer, steel-blue clay is found at least to a depth of 14 in. below the surface. Animal burrows are abundant in the upper layers.

One notably variable climatic factor during the field work was precipitation. The year 1957 was dry with rainfall of 35.27 in. or 8.76 in. below normal. In contrast, 1958 was unusually wet, with 49.81 in., 5.78 in. higher than normal. (Rainfall and temperatures are shown in Fig. 5.)

The field plot

A 70 × 90 ft plot, set up paralleling "Spooky Brook," a small intermittent stream that dries up almost every summer, was marked off in a 10-ft grid system (cf. Figs. 1 and 4).

Natural cover for salamanders consisted of pieces of logs of all sizes and in all states of decay, and leaf litter which almost completely covered the soil except where washed away by the occasionally-swollen stream. The pieces of logs were considered to be shelter objects and were arbitrarily classified as movable or non-movable. Those classified as non-movable were logs too heavy to be moved, pieces of dead roots partially on the surface and partially imbedded in deep

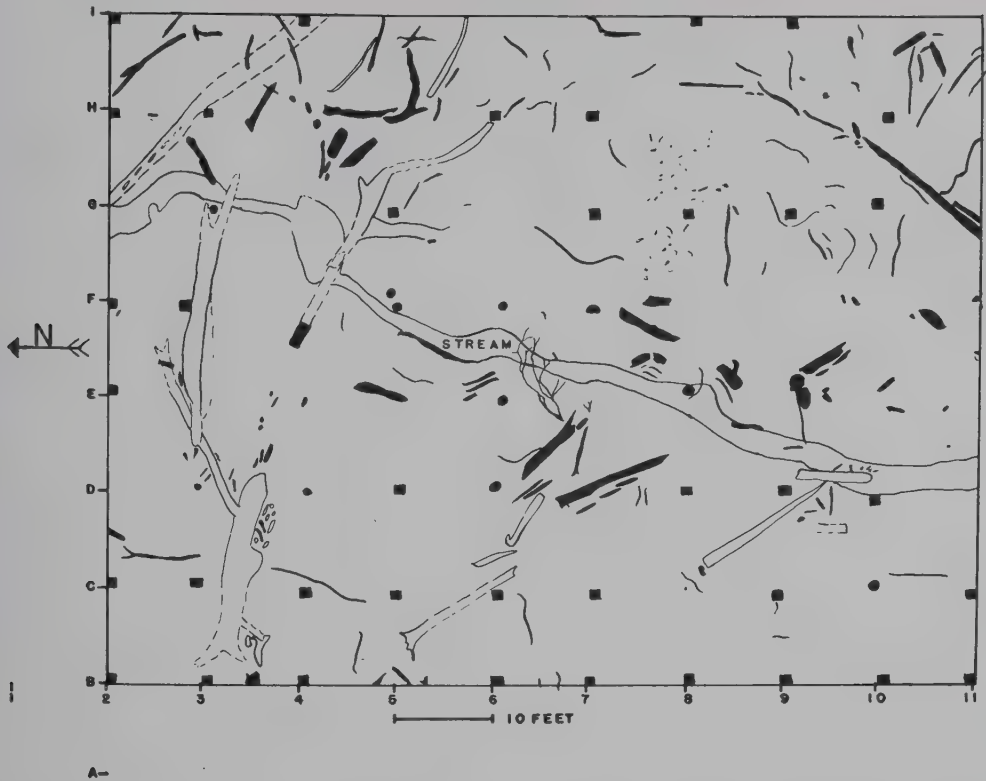


FIG. 1. Map of the research plot showing the grid system and the cover. Solid forms represent movable shelter objects and open forms represent non-movable shelter objects. Dotted lines represent logs which are suspended above the soil. The sizes and shapes of natural shelter objects are shown. Squares represent experimental shelter boards, circles represent experimentally placed rocks.

soil, and fragments too small and too numerous to move; this totaled 153 ft² within the plot. Movable cover, which could be turned for routine examination, totaled 187.5 ft². The distribution of movable and non-movable cover is shown in Figure 1. Leaf litter was not mapped because the amount varied from place to place seasonally. Roots of living plants were not counted as cover although there is no reason to suspect that they could not serve in this capacity. Logs suspended over the soil, but not touching the surface, were not counted as cover.

To this natural cover were added 39 pine boards 12 × 10 × 1 in., and one similarly-sized piece of tar paper. These were placed at grid points throughout the plot but especially in the areas deficient of natural cover. Eight stones, each approximately ½ ft² in area, were used along the stream in place of boards. These experimental shelter objects were placed during October and November 1955. Thus a total of 340.5 ft² of natural, and approximately 44 ft² of experi-

mental, shelter occurred in the area during the study.

Between November 1955 and November 1958 119 searches of the plot were made. A single search consisted of over-turning the movable natural shelter objects and the experimental shelter objects and examining the surface of the object and the litter beneath it for salamanders. The entire plot was searched in a minimum length of time, usually one to 2 hours. These searches were made during all hours of the day and night.

Other areas were sampled less frequently than the plot. An area immediately outside of the plot, designated as I-1 was searched as completely and frequently as the plot after the spring of 1956. This area measured approximately 500 ft² and contained 37 ft² of cover, all natural and movable. The periphery of the plot was frequently searched. Occasionally searches were made in the remainder of the forest.

Adults from the plot were measured, marked, and released. A salamander was measured by

placing it on a card and prodding it gently into a suitable position. The position of the head, vent (estimated) and tip of tail were marked on the card and measured in the laboratory. This proved to be as accurate as stretching the animal along a ruler edge and it was less time consuming and required less handling. The method was accurate to within ± 2 or 3 mm for an 80 mm salamander. At this time the general condition of the animal, the location, and time of capture were noted.

Each individual was numbered by means of toe clipping. All but the smallest *Plethodon* could be marked in this manner. Despite the possibility of non-recognition of a marked animal because of the regeneration of clipped toes, toe clipping is the method recommended by Woodbury (1956) after a review of marking methods. A method of suturing was attempted, but abandoned. The animals were released at the point of capture within 5 minutes of capture.

The temperature was measured at the beginning and/or end of each search. These readings were taken at grid position A₂ at the base of a tree and on the surface of the litter. From November, 1955 to June, 1956 a thermistor was used; later a rapid-reading mercury thermometer was used. Temperatures were also taken at many of the capture sites by means of a rapid-reading thermometer. A set of maximum and minimum thermometers was left in the plot or in the cages to measure the range of temperature on the floor of the forest.

From September, 1956 to the end of the study, soil samples were taken from the majority of the capture sites. This was done by collecting 20-30 grams of soil from the exact location of the salamander capture. The soil was placed in a small vial, corked, brought to the laboratory, uncorked, weighed, dried in an oven slightly above 100°C for at least 24 hours, and reweighed. The soil moisture was expressed in terms of weight of water per weight of dry soil.

Underground field cages

Four underground cages were installed approximately 15 ft from "Spooky Brook" near the research plot. The soil in this area was that of the stream flood plain. The cages were buried to a depth of 12 in. and extended 6 in. above the soil. The cages (Figure 2) were made of plastic Saran mesh (16 threads per in.) with wooden supports. Originally the tops were fastened with eyelets and hooks around the wooden edges, but later heavy duty brass zippers were used and found to be more satisfactory. To prevent mammals from burrowing through the sides, the 4 cages were

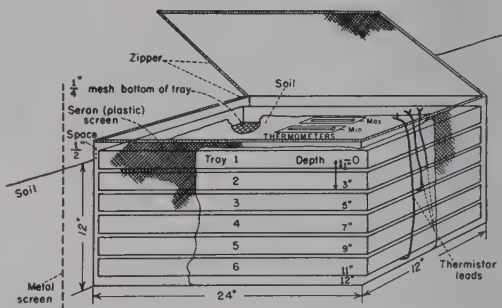


FIG. 2. Underground field cages used to study vertical *Plethodon* distribution under semi-natural conditions.

placed within an enclosure of hardware cloth that extended 14 in. below ground and 10 in. above ground level. The cages were arranged 6 inches apart in the form of a square.

Two of the cages were fitted with trays through which salamanders could pass but which would support the soil. Each tray was made of wooden sides, 2 in. high and $\frac{1}{2}$ in. in thickness, with an open mesh bottom. Originally a rayon "fish net" curtain material was used, but this had to be replaced each month because of rotting. In 1958 galvanized hardware cloth of $\frac{1}{4}$ in. mesh was used after it was ascertained that the metal was not toxic to *Plethodon*. The length and width of each tray was such that it fit somewhat loosely into the plastic mesh cage. Six such trays were fitted one on top of another into the bottom of each of the cages. The cage and tray design is shown in Fig. 2. The salamanders were able to move about, between, and along the sides of the trays with little difficulty. Thus they had access to the depths of the soil either by burrowing through soil and mesh or by moving down the sides between the Saran mesh and the tray sides.

Instruments were buried in one of the trayless and one of the trayed cages when they were filled with soil. Thermistor elements were buried at the 3 in., 6 in., and 12 in. levels. During 1957 gypsum soil blocks were buried at the 3 in. and 12 in. levels to measure vertical moisture gradients. The thermistor elements and gypsum blocks were read with an A. C. ohmmeter. In 1958 soil samples were taken to measure the soil moisture in place of the gypsum blocks.

Ten *Plethodon cinereus*, collected from other locations in New Jersey, were placed in each of the four cages. These were replaced as animals died or escaped.

The trayless cages were sampled by quietly opening the lid, searching the top inch of soil and litter, recording any captures, and taking in-

strument readings. The trayed cages were sampled as follows: a large sheet of plastic was spread on the ground beside the cage; the trays were removed as rapidly as possible, and stacked with plastic interleaves; the trays were then individually searched and salamander captures were recorded as to tray number. The mean depth was calculated on the basis of the tray numbers in which the salamanders were found. Thus all salamanders found in the top tray, whether on top or under the litter were counted as being in tray 1. The salamanders were replaced in the trays in which they were found, and the trays were replaced in their original order.

The cages were sampled immediately before and/or after the natural plot was searched during the fall of 1957 and during the summer and fall of 1958, and once during April, 1959. Hibernation survival was measured for the winters of 1957 and 1958.

Mazes—an experimental substrate

Plaster of Paris mazes were constructed as a means of observing the vertical distribution of *Plethodon* within a simulated soil environment which required neither handling of the animals nor destroying the environment for each observation (Figure 3). The surface was exposed to light and dark cycles while tunnels below the surface were dark except for brief periods during observations. Within the mazes the changes in salamander distribution in response to various moisture and temperature gradients were measured.

Each maze was molded and used in a 10 in. diameter battery jar coated with a thin layer (ca.

mm) of paraffin. A tall jar of 6 in. diameter was coated with petroleum jelly and placed in the center of the battery jar. Small plugs of plaster (molded from wax casts of size 2 rubber stoppers) were attached to the center jar and covered with petroleum jelly. (These plugs were intended as a means of measuring the percentage of moisture). Plaster of Paris was mixed with half its volume of water and poured into the battery jar to a depth of 2 in. This was permitted to harden, and the surface was coated with petroleum jelly. Three additional layers were poured in this manner so that the depth of the maze was 8 in. The battery jar was then turned upside down and heated so that the paraffin melted. Thus the plaster layers were removed from the glass jar. The 4 layers were then separated and cleaned. Grooves of approximately 1 cm diameter were gouged around the circumference so that they formed tunnels, or burrows. The glass formed one wall of the burrows when the mazes were placed in the battery jars. A horizontal groove was gouged in the center of each of the 4 layers and 11 vertical grooves were gouged the depth of the 4 layers. The center cavity, which remained after the inner jar was removed, provided access for instruments. This was covered with a thin layer of plaster which provided a complete surface for the salamanders. The small plaster plugs were removed, cleaned, and replaced. In use, the battery jar was covered by a black plastic cover up to the top of the plaster. The mouth of the jar was covered with a fine netting of nylon and, in later experiments, with hardware cloth.

Moisture gradients were determined at the time the mazes were set up. Two qualities of moisture were used. "Wet" was a layer soaked to take up a maximum amount of water, which required 10-15 minutes, and drained for at least 30 minutes, until it no longer dripped. "Dry" was air-dried for greater than 1 month after construction. During the course of an experiment there was a slight tendency for the dry layers to gain water while the wet layers lost water. The tendency to gain water was greater for the bottom layers.

Moisture conditions were as follows:

- wet/wet Uniformly wet—all 4 layers soaked.
- wet/dry Top 2 layers wet, bottom 2 dry.
- dry/wet Top 2 layers dry, bottom wet.

The heating equipment, installed in 3 of the mazes consisted of 660 watt Nichrome heating elements placed in heat resistant and waterproof plastic tubes. Two were placed in each maze, one between the first and 2nd layers, and the other

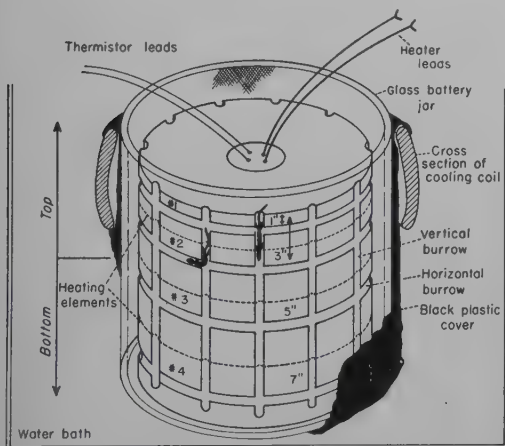


FIG. 3. Experimental mazes used to study vertical *Plethodon* distribution under controlled simulated soil conditions.

between the 3rd and 4th layers. Canals were gouged out to hold the tubes so that the layers fitted snugly together again. Electricity was supplied through a transformer, usually at 10 to 15 volts, to either the top or bottom heaters of the 3 mazes in parallel.

Two types of cooling equipment were used. For bottom cooling the battery jars were placed in a running cold water bath to a level between layers 2 and 3. For cooling the tops of the mazes, plastic tubes of 2 in. diameter (made by heat sealing sheet plastic) were held against the battery jars by hardware cloth frames. The frames were covered with black plastic and the usual black cover came up to the bottom of the cooling frame. The temperature conditions were designated as follows:

TA	seasonal temperature, no superimposed gradient.
hot/cool	hot on top, cool on the bottom.
cool/hot	cool on top, hot on the bottom.
TB	seasonal temperature, no superimposed gradient.

Two thermistor elements were placed in one of the mazes at the top and bottom layers. Occasional checks were taken with mercury thermometers in the other mazes.

The 3 mazes with heating equipment were kept in a greenhouse and were subject to seasonal light cycles and temperature conditions, as a base upon which temperature gradients were superimposed. For each experimental run one of these mazes was set up under wet/wet, one under wet/dry and one under dry/wet moisture conditions.

One maze, which served as a control, was kept under the same temperature, lighting conditions, and moisture wet/wet, during all experimental runs. Temperature control was maintained by a constant temperature incubator placed within a constant temperature coldroom. The temperature within the incubator was maintained at $18^{\circ} \pm 2^{\circ}\text{C}$. The light cycle was regulated by a time switch to give 12 hours of light beginning at 0600 EST and 12 hours of dark. The light was supplied by a 6 watt Westinghouse bulb. (The November control sample was run with a 6 watt General Electric bulb which gave off more heat; for this reason the November control data have not been used). During the "day" the top of the maze was a few degrees warmer than the bottom, where the temperature was measured.

For each experimental run 12 salamanders were put on the surface of each of the 4 mazes on day zero, and left without the superimposition of temperature gradients (TA), until day 3, at

which time observations were made at 1400 and 2000 EST. At the end of the 2000 EST observation, the 3 greenhouse mazes were subjected to cooling on the bottom and heating toward the top to produce the hot/cool condition. The mazes were maintained in this condition from the evening of day 3 through the evening of day 5, when observations were made at 1400 and 2000 EST. After the 2000 EST observation, the greenhouse mazes were subjected to heating on the bottom and cooling toward the top to produce the cool/hot condition. Observations were made of the T3 condition on day 7 at 1400 and 2000 EST. At the conclusion of T3 condition all temperature regulation was ended, and greenhouse mazes were permitted to obtain a uniform temperature (TB), which was usually similar to the first temperature condition. This was maintained until day 10 when the final pair of observations took place. Observations of the control were made immediately after observations of the greenhouse mazes. Thus each moisture condition was subjected to the same regime of temperature conditions, and the control and the 3 moisture conditions in the greenhouse were observed almost simultaneously.

Observations were made by lowering the black plastic cover and gently rotating the maze. The position of each salamander was sketched on a data sheet. Temperature conditions within the mazes were measured immediately after the observations. At night a 6 volt headlight was used for observations. The horizontal burrows were used as depth indicators, level one being 1 in. below the surface; level two, 3 in. below the surface; level three, 5 in. below the surface; and level four, 7 in. below the surface. Thus a depth of 2.5 indicates that the center of a salamander's body was between the 2nd and 3rd horizontal layers, or 4 in. below the surface.

The mazes were cleaned and soaked for each month's run. The following runs were made: 2 simultaneous runs in February (wet/wet, without temperature gradients); early May; late May; July; August; September; October; November; and December. With 2 exceptions the salamanders for each run were captured within 2 days of beginning of the run. The salamanders used in the February runs had been in captivity all winter, and the animals used in the December run were mostly those that had been used in November. The salamanders for each maze were selected randomly from the fresh captures of *Plethodon* of more than 40 mm head to tail length taken from various parts of New Jersey.

RESULTS

Horizontal distribution and movement in litter

One hundred nineteen routine searches of the research plot yielded 145 captures of *Plethodon c. cinereus*, 118 *Eurycea b. bislineata*, and 3 *Pseudotriton r. ruber*. Within the I-1 and peripheral areas 83 *Plethodon*, 24 *Eurycea*, and 4 *Pseudotriton* captures occurred. These were the only species of salamanders found in the forest. Of the *Plethodon* captures, 5.4% were of the red phase and the remainder were of the dark phase.

The horizontal distribution of captures within the plot is analyzed with respect to the stream in Figure 4. The plot has been divided into two areas, (1) the stream and vicinity, a strip 30 ft in width which constitutes 43% of the plot, and (2) the area away from the stream, which is 57% of the plot. If the salamander distribution was independent of the stream, approximately 43% (62) of the captures should be in the vicinity of the stream, whereas only 49 of the 145 *Plethodon* captures actually occurred near the stream. A Chi-Square test, showed significant differences between observed and expected frequencies ($\chi^2 = 4.8$, d.f. = 1, $p < 0.05$).

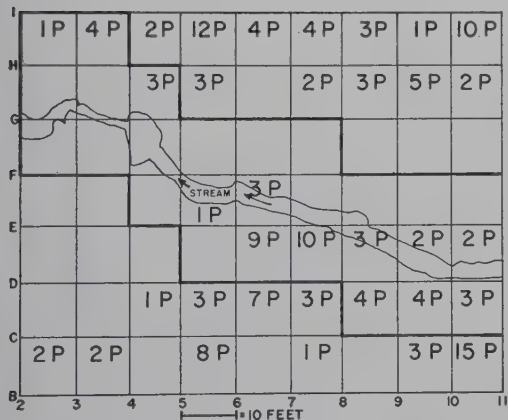


FIG. 4. Chart of the research plot showing the horizontal distribution of captures.

One hundred fifty-four *Plethodon* were marked. Twenty-four individuals were recaptured; 20 were recaptured only once, 1 was recaptured twice, 2 were recaptured 3 times; and 1 was recaptured 4 times. At the conclusion of the study the majority of the salamanders captured showed no signs of having been marked.

The horizontal movements of the animals are shown by the distances moved between captures of marked animals. Twenty-seven measurements were taken between capture sites of 20 *Plethodon* individuals. There were 14 distances of less than

1 ft (usually under the same object as the previous capture), 4 of 1-5 ft, 5 of 6-10 ft, 1 of 11-15 ft, and 3 of greater than 16 ft distance moved between captures. There was no correlation between the number of captures of an individual and the greatest distance between captures. The direction of the movements and the searches of the peripheral area gave no indication of immigration into, nor emigration from the plot.

Several searches of the plot frequently occurred between recaptures of marked individuals. A mean of 10 searches occurred between successive captures, the maximum being 56 searches of the plot; on the 57th search this specimen was found under the same object from which it had originally been captured 11 months previously. There was no correlation between the length of disappearance and the distance moved.

Effects of environmental factors on occurrence in the litter

Under natural conditions the vertical movements and resulting distribution can best be inferred by the abundance of litter captures (assuming a stationary population size). The captures are shown in control chart form in Figure 5 along with the temperature of the forest floor and the rainfall as recorded at the New Brunswick Station of the U. S. Weather Bureau. The control chart method is a statistical means of deciding whether variation is due to "chance" or are larger than would be expected due to chance alone. A point falling outside of the control limits at ± 3 standard deviations has a probability of occurrence of less than 0.01 and is said to be due to an "assignable cause." The chart here is based on a Poisson distribution because, according to Dice (1955), frequency of capture data best fit this kind of curve. For example, if the distribution is random, the number of samples in which 0, 1, 2, . . . are counted will fall into a Poisson series. This method is number 16 as described in the ASTM manual on Quality Control of Materials (1951).

Plethodon captures increased through spring, sharply decreased through the summer, and then increased sharply in the autumn in 1956 and 1958. The higher *Plethodon* captures/search tended to be made as the temperature increased during spring and as it decreased during autumn. Temperature readings taken by a rapid-reading thermometer at salamander capture sites were usually within 1°C and never more than 2°C of the temperature taken at the surface of the litter at the A₂ grid position. Therefore the A₂ grid temperature is an approximate measure of the tem-

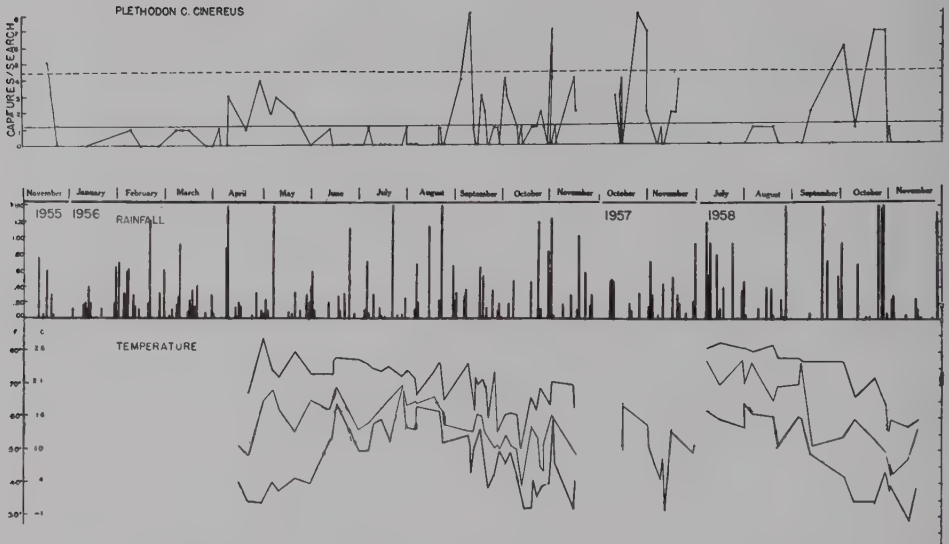


FIG. 5. Control chart of *Plethodon* captures, compared with daily rainfall, from U.S. Weather Bureau summaries, and temperature on the forest floor. The control chart refers to the numbers of captures made during each search. The center line represents the mean. The dotted line is the upper control limit at $+3$ standard deviations. The lower control limit for both species is 0 captures / search. In the temperature graph, the heavy lines are the maximum and minimum temperatures; the lighter line represents the temperatures at which the searches were made.

perature of all the captures made during a given search. When the number of salamanders captured at each temperature is divided by the number of searches at that temperature, any bias is removed which might have been introduced by sampling any temperature a disproportionate number of times (Figure 6). Captures occurred from 5°C to 25°C with a mean of 13.3°C ($s =$

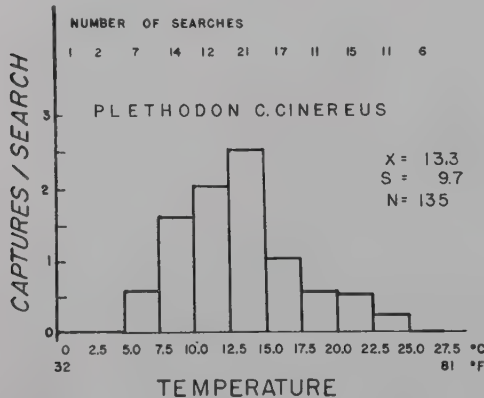


FIG. 6. Average captures per search with respect to temperature. The number of animals found at each temperature has been divided by the number of searches at that temperature.

9.7, $n = 135$). The distribution is skewed toward the lower temperatures.

It may be noted in Figure 5 that heavy rainfalls frequently, but not invariably, preceded unusually high numbers of captures/search. For example the heavy rains during July and August did not result in high captures of *Plethodon* during 1956 nor during 1958.

The soil moisture (weight of water $\times$ 100/weight of dry soil) of salamander capture sites

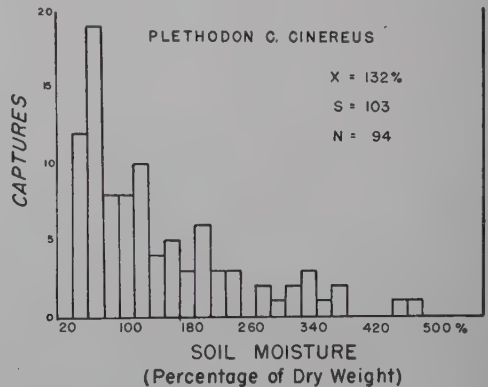


FIG. 7. Histogram of captures with regard to soil moisture.

(Figure 7) had a mean of 132% ($s = 103$, $n = 94$). The very great amounts of water reflect the high organic content of the surface soils.

The data show a mean of 1.129 captures/search ($s = 1.74$, $n = 77$) during the day as compared to 1.38 captures/search ($s = 2.19$, $n = 41$) during the night. These means were not significantly different ($z = 0.72$, $P = 0.22$).

Twenty % of the 1956 *Plethodon* captures were estimated as having hatched that year on the basis of size distribution. In 1957, an unusually dry year, only 6.5% of the captures were in the first year class. In 1958, 30% of the captures were estimated as being in the first year class.

The experimental cover yielded more salamanders per square foot (mean of 1.20) than the natural cover (.50).

Vertical distribution

Within the trayed cages *Plethodon* moved downward to the full depth of 12 inches. The average depth for the entire study was 5 in. (tray level 3.5). The mean depth for 1957 was 7 in. (tray level 4.6) while that of 1958 was 2.8 in.

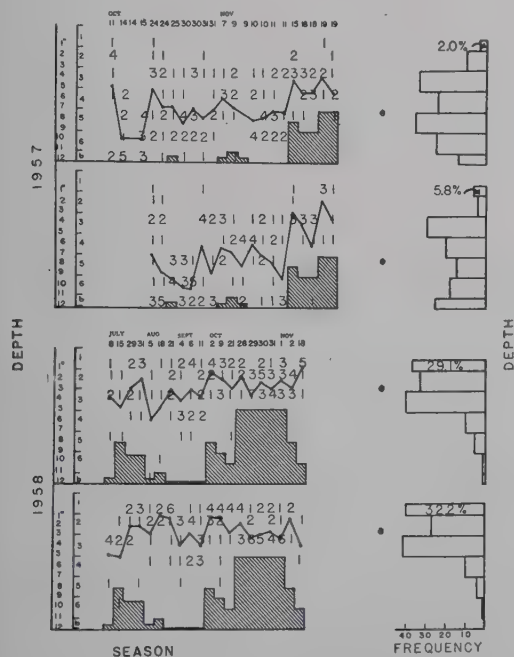


FIG. 8. Vertical distributions of *Plethodon* in the trayed underground cages. Two cages were run simultaneously. Each number represents the number of salamanders found in that tray during a single observation. The circled dot represents the average depth for each cage for each year. Summated distributions are shown to the right. The percentage of salamanders found in the surface tray (top inch of litter and soil) is indicated. The slanted lines represent the water table.

(tray level 2.3). As shown in Figure 8, the overall pattern of distribution was higher in 1958 than in 1957. The known differences between the 2 years were: (1) rainfall and therefore water table level, and (2) the addition in 1958 of bark to the natural leaf litter. Environmental factors appeared to influence the vertical distribution since trends, as shown by the changes in the means, frequently corresponded in the 2 trayed cages that were run simultaneously. The environmental factors considered were daily light-dark cycle, temperature, water table level, and soil moisture.

There was no diurnal difference in vertical distribution as shown by the means of night and day searches, both means being 3.5. More *Plethodon* were found on top of the litter at night, but there was no shift toward the surface in the overall vertical distribution. During part of 1957, equal numbers of searches were made during 4 time periods, 0000-0550; 0600-1150; 1200-1750; 1800-2350 EST (Table I). A slight tendency was noted for the distribution to be nearer the surface during the 0000-0550 period.

TABLE I. Vertical distribution of *Plethodon* during 4 time periods. Several searches have been summed for each time period

Depth in.	Tray no.	TIME PERIOD, EST			
		0000-0550	0600-1150	1200-1750	1800-2350
1	1	3	1	0	1
3	2	5	5	0	1
5	3	20	13	12	10
7	4	8	12	15	14
9	5	11	15	14	15
11	6	10	14	15	15
12	b	15	14	11	0

However, the vertical distributions of these time periods were not significantly different as tested by a Chi-square test of homogeneity ($\chi^2 = 15.66$, d.f. = 9, $P = 0.07$). The temperature range studied was -6°C to 25°C . Temperature seemed to have an effect only at the lower end of this range, as shown in Figure 9. No salamanders were ever found at temperatures below 4°C although such temperatures were sampled 15 times. Immediately above 4°C captures were common, although there was a tendency for salamanders to avoid all temperatures below 10°C if a higher temperature occurred in the cage. No avoidance was noted at the upper end of the temperature range studied. The temperature range over which *Plethodon* were found here, $4^\circ\text{--}25^\circ\text{C}$, agrees almost exactly with the range over which *Plethodon* were captured in the research plot, $5^\circ\text{--}25^\circ\text{C}$.

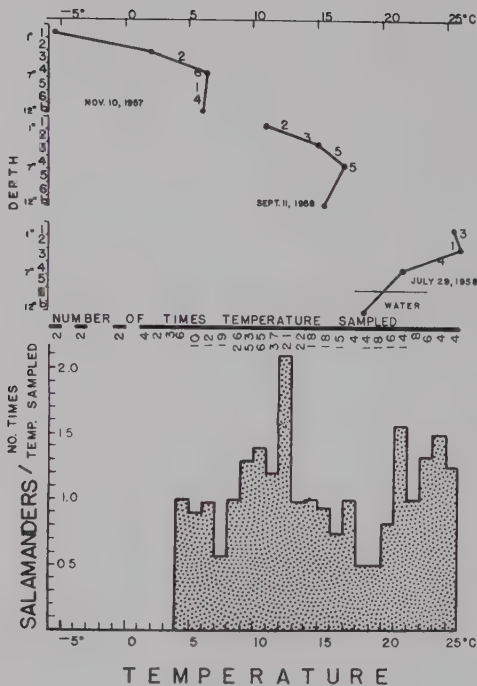


FIG. 9. *Plethodon* distribution in the trayed cages with respect to temperature. The histogram shows the frequency of capture at each temperature divided by the number of times that temperature was sampled. The temperatures sampled and the number of times each temperature was sampled is illustrated above the histogram. The salamander distributions over 3 temperature ranges are shown in the upper half of the Figure as samples of the raw data. Each number represents the number of salamanders found at that depth and temperature. The line represents the range of temperatures as measured at the surface, 3 in., 6 in., and 12 in. levels.

There was a definite avoidance of levels which were below the water table (Fig. 8). As the water table rose, in both 1957 and 1958, the entire distribution was shifted upward. Even after the water table dropped in November, 1958 the salamanders did not rapidly reoccupy the formerly inundated soil. Occasionally salamanders dropped from the sides of the trays into the water and remained there for several minutes but they always returned if the cages were not disturbed for a few minutes.

Study of the vertical distribution of soil moisture is a complex problem. Soil moisture is best discussed in terms of the tenacity with which soil water is held or the force necessary to remove water from the soil (Lutz and Chandler 1946). The percentage of water found in the soil is not necessarily a meaningful measure, since soils of

different locations and of different depths at the same location are saturated at different percentages and will hold soil water with different tenacities. Thus at the site of the cages, the soil of the first 5 in. is saturated at 61.2% soil water, while the soils at depths of 6-10 in. and 11-15 in. are saturated at 35.5% and 28.6% respectively. The surface soils will also yield water more readily than the lower layers as shown in Table II. The soil in the cages was almost always saturated and the methods used here did not give as sensitive a measure as would be necessary to relate slight changes in the vertical pattern of soil moisture to the salamander distribution.

TABLE II. Water relations of the soil at the cage site (poorly drained). The percent of moisture is the amount of soil moisture remaining in the soil after extractions at tensions indicated by pF. pF is the logarithm of the height in centimeters of a column of water equivalent to the force with which moisture is held at the air-soil surface. Each value is the mean of 6 samples

Depth (in.)	% SOIL WATER			
	at saturation	pF		
		1.8 (60 cm.)	2.5 ($\frac{1}{2}$ atm.)	3.0 (1 atm.)
1-5.....	61.2%	46.0%	44.4%	43.1%
6-10.....	35.5	27.0	25.7	24.1
11-15.....	28.6	27.1	26.5	26.0

Population estimates based on litter captures

Population estimates based on litter, results of the trayed and trayless cages during a one week period, were analyzed as described by Hayne (1949). This uses a mark and release method to estimate the population by following the increase of the proportion marked in samples drawn from the population as additional animals are marked. The data and calculations are shown in Table III. In the 2 trayless cages, estimates of 11.8 and 9.9 salamanders were obtained when 10 *Plethodon* had been placed in each of the cages at the beginning of the study and 9 were recovered from each of the cages at the end of the study. In the trayed cages, estimates of 4 and 4.4 salamanders were obtained when 10 *Plethodon* had been placed in each of the cages at the beginning and 8 and 9 respectively, were recovered in each at the end of the study. The low estimates result from the fact that some individuals tended to remain on or near the surface while others were not captured on the surface at all. Thus in each of the trayed cages only 3 individuals were found on the surface during the 4 searches, while 5 and

TABLE III. Record of surface captures in trayed and trayless cages, and calculation of population size estimates (estimated population, $P = \frac{wx^2}{wxy}$)

Cage number	NUMBER OF CAPTURES			Proportion of catch previously handled (y)	Total no. previously handled (x)
	Total (w)	New	Old		
#1 (trayless) true population = 9-10	6	6	0	0	—
	3	1	2	.50	6
	9	2	7	.78	7
	3	1	2	.33	9
	P = 11.8				
#2 (trayless) true population = 9-10	2	2	0	0	—
	2	1	1	.50	2
	1	1	0	0	4
	3	2	1	.33	5
	P = 9.9				
#3 (trayed) true population = 8-10	0	0	0	0	—
	2	2	0	0	0
	1	0	1	1.00	2
	3	1	2	.33	2
	P = 4.0				
#4 (trayed) true population = 9-10	1	1	0	0	—
	2	1	1	.50	1
	2	1	1	.50	2
	1	0	1	1.00	5
	P = 4.4				

6 individuals were not found on the surface. In the trayless cages, which gave fairly accurate estimates, 10 individuals were captured on the surface of one, and 6 were captured on the surface of the other.

Comparison of plot and cage distributions

In an attempt to see if there was a relationship between the results in the experimental field plot and the results in the experimental field cages, the plot results were compared (1) with the surface results of the trayed cages, and (2) with the mean depth of salamanders in the trayed cages. For each day of observations, the number of captures of *Plethodon* within the plot was charted against the percentage of salamanders found near the surface in the trayed cages. A table of frequencies was prepared from this chart, Table IV, and the frequencies were compared by a Chi-square test of association (Simpson and Roe 1939). The data do not suggest that a large number of captures in the plot are associated with a large percentage of salamanders on the surface in the cages ($\chi^2 = 0.118$, d.f. = 1, $P = 0.85$). A similar test between the number of captures in the plot with the mean depth in the cages also failed to suggest that a mean depth near the surface was associated with large numbers of captures of *Plethodon* in the plot, Table 5 ($\chi^2 = 0.238$, d.f. = 1, $P = 0.60$).

TABLE IV. Comparison of the number of searches of the plot with and without captures with the percentage of the trayed cage population found on the surface

Plot	CAGE % of population found in surface tray	
	Less than 10%	10% or more
0 captures	9	10
Greater than 0 captures	8	7

TABLE V. Comparison of the number of searches of the plot with and without captures with the mean depth of the salamanders in the trayed cages

Plot	CAGE § lower than 5 in. § higher than 5 in.	
0 captures	8	8
Greater than 0 captures	10	7

Winter survival

Four and 6 *Plethodon* respectively, survived the winter in the 2 trayed cages. Ten salamanders had been left in each of the cages from November 22, 1957 to June 1958. The vertical temperature distribution was found to range from -6°C to 2°C during 2 checks in February, 1958. No salamanders survived the 1958 winter, which was colder with less snow.

Vertical distribution under controlled environmental conditions

When the salamanders were placed on the surfaces of the mazes, they wandered about briefly and then entered the tunnels, usually within 10 minutes. Preliminary studies showed that they were spread throughout the mazes at the end of 2 days. The overall distribution of the salamanders was measured by the mean depth in terms of tunnel levels. The mean depth values at each observation of each of the mazes are shown in Figure 10. The trends can best be seen in the results of July, August, and September. Under uniform temperature (TA) the salamanders were close to the surface in the wet/dry maze (wet top, dry bottom), near the bottom in the dry/wet maze and spread throughout the entire maze in the wet/wet maze. After the hot/cool condition had been superimposed for $1\frac{1}{2}$ days, the salamanders had moved downward in all of the mazes. After the temperature gradient was reversed, cool/hot, the salamanders moved upward. After all the temperature gradients were removed

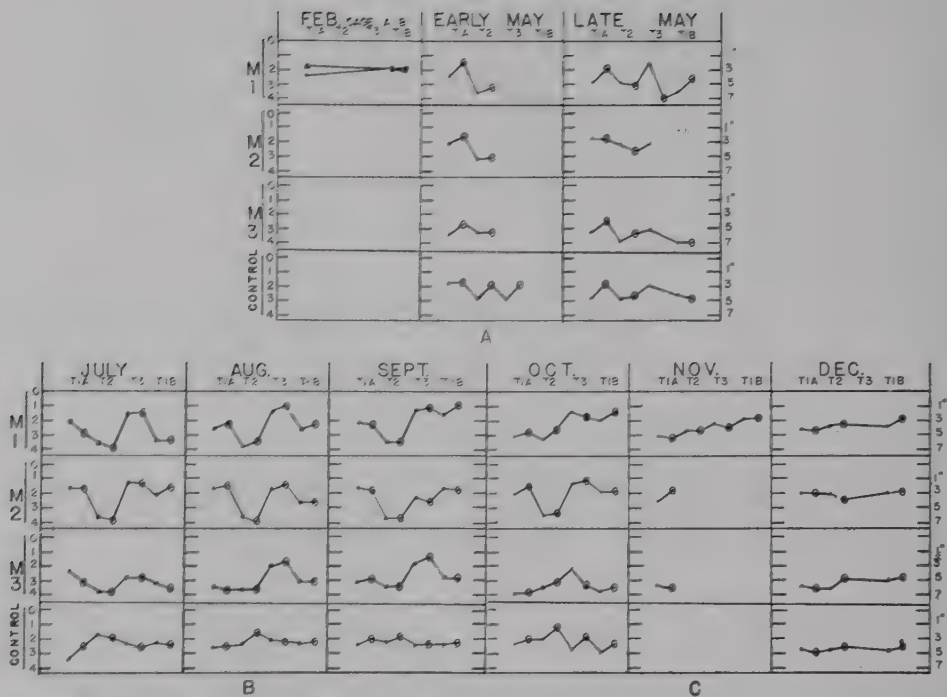


FIG. 10. Mean depth of each observation of each run of salamanders in the mazes. Dots represent day observations, and circled dots represent night observation. All points within a vertical line were taken within one hour. The depths are given both in inches (right) and in terms of the horizontal burrows (left). The environmental conditions are indicated as follows: T1A seasonal temperature, no superimposed gradient; T₂, hot/cool; T₃, cool/hot; T1B seasonal temperature, no superimposed gradient (10 days after T1B); M1, wet/wet; M₂, wet/dry; M₃, dry/wet.

(TB) and the mazes left for 2-½ days, the distribution shifted toward the original TA pattern, but was typically nearer the surface, showing some lag from the cool/hot condition. During the cooler months (spring and fall) the temperature effects were less extreme. The distributions of salamanders in the control maze were relatively constant.

The effects of the 10 day captivity, season, temperature, moisture, and light have been analyzed. The data have been presented and analyzed in an analysis of means (Figure 11), as described by Ott (1958), but slightly modified to handle unequal sample sizes as given in the ASTM manual (1951). One use of this method is to compare the effects of different factors and/or different levels of factors upon the variation in results. The method consists of summing the results of all runs under each condition and comparing the means of each condition by a control chart. The control limits are based upon the normal distribution and are drawn at $\bar{X} \pm 3$ standard deviations of the means.

To test whether there was any effect upon the vertical distribution due to the salamanders being in the mazes for 10 days, the first day observations in the control maze were compared with the observations of the 10th day. No significant differences were found.

The overall analysis for seasonal effect is somewhat misleading because the experiments in several of the months lacked the complete series of temperature gradients (February, early May, late May, November, and December); this tended to skew the results. Thus February and May results appear to be significantly higher and lower, respectively, than the rest of the means largely because no temperature gradients were imposed during the February run, and each of the May runs lacked a complete cool/hot gradient for both day and night. To remove the effect of incomplete runs, the seasonal effects were compared under the TA, uniform temperature, wet/wet, light condition, which was taken for each of the months studied. Using these data the monthly mean vertical distributions are not significantly

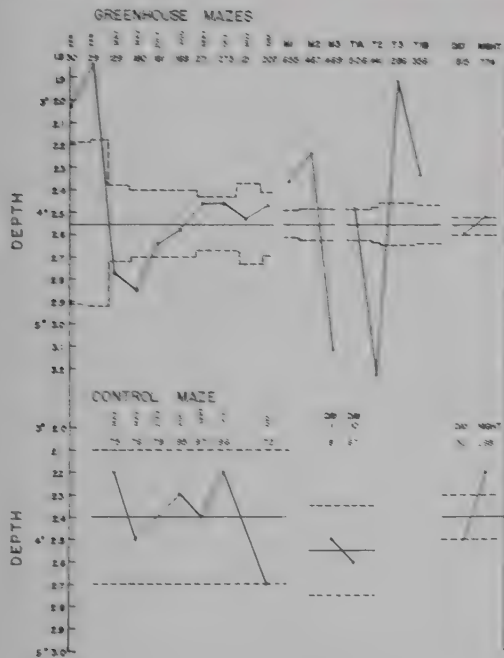


FIG. 11. Control chart of mean depth of salamanders for total maze data. Letter symbols as in Fig. 10. The heavy center line is the mean. The dotted lines are the control limits at ± 3 standard deviations. The number above each point represents the salamander observations upon which that point is based.

different from each other. Under the control conditions, no significant differences were found in the vertical distributions of the various months.

A seasonal difference was seen in the surface occurrence, although not at a significant level. Occurrences tended to be high in spring and fall, and low in summer in both the greenhouse and the control mazes. This is especially noteworthy in the control maze since only the animals, but not the environmental conditions, varied seasonally.

Moisture gradients significantly affected the vertical distribution of *Plethodon*. The salamanders avoided the dry layers if no temperature gradients were superimposed. This is most evident under uniform temperature (i.e., seasonal temperature, with no vertical gradient). The wet/dry maze had a significantly higher distribution (2.6 in., $n = 161$) and the dry/wet had a significantly lower distribution (5.5 in., $n = 166$) than did the wet/wet maze (3.9 in., $n = 192$).

Temperature gradients also significantly affected the vertical distribution. The effect of temperature alone is most evident when the wet/wet condition is considered, the average depths being,

TA 4.0 in. ($n = 192$); hot/cool 5.3 in. ($n = 166$); cool/hot 2.5 in. ($n = 126$); TB, 3.1 in. ($n = 171$). Under most of the temperature ranges used, the salamanders moved toward the cooler end whether it was in the upward or downward direction. Because seasonal, and therefore different, temperatures were used in the greenhouse mazes, it is necessary to examine each temperature range separately (Fig. 12). Here the results of the hot/cool condition are shown because the temperature ranges used were wider than under the cool/hot condition. When the temperature exceeded 18°C the salamander distribution was skewed toward the lower temperature. The higher the temperatures, the more sharply the distribution was skewed. *Plethodon* was never found above 27°C although the ranges of July, August, and September extended up to or beyond this temperature. When the minimum temperature was below 15°C , there was a slight tendency to move away from the cool end. Essentially the same results were seen when the direction of the gradient was reversed. Thus there was no indication that the salamanders moved downward any more readily than upward in response to similar temperature gradients.

As an indication of the sensitivity of *Plethodon* to temperature, the distribution was skewed when the gradient had a range of only 1.5 and 2.0° , and where the lowest temperature was above 18°C under cool/hot conditions.

The distribution under TB tended to be significantly higher than at TA although similar temperatures prevailed under both conditions (Fig. 11). It appears that the raised distribution due to heating the bottom under cool/hot conditions carried over for the 3 day period after the temperature gradient was removed.

The wet/dry and dry/wet mazes measured the interaction between moisture and temperature gradients. In these mazes salamanders avoided the dry layers if no temperature gradient existed or if the temperature of the dry layers was above that of the wet layers. Under both moisture conditions there were a tendency to move onto the dry layers if they were cooler and if the wet blocks exceeded $18^{\circ}\text{--}20^{\circ}\text{C}$. Thus the same temperature which caused movement from hot-wet layers to cool wet layers sufficed to cause movement from hot-wet layers to cool-dry layers. No salamanders were found on layers which exceeded 27°C . (Condensed water on the glass somewhat alleviated the dry condition, but the plaster gained very little water. Occasionally condensed water collected at the bottom of the mazes). When the temperature gradients were re-

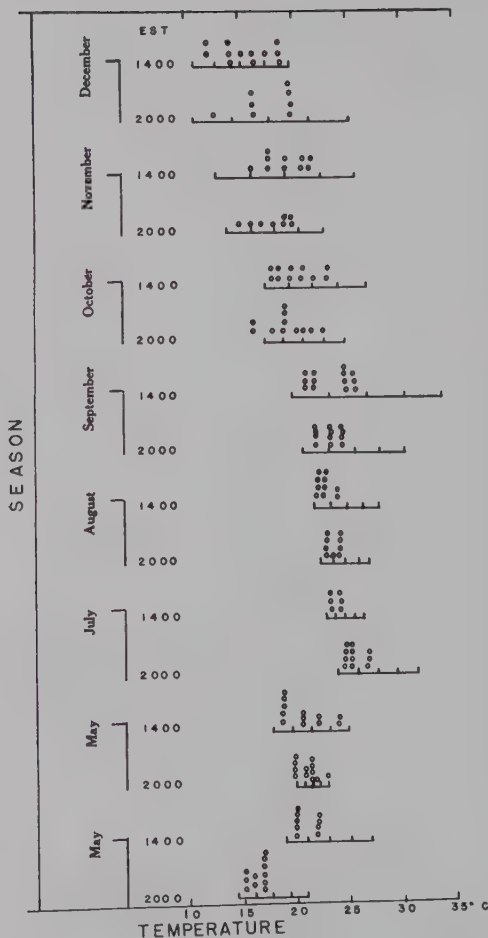


FIG. 12. Distribution of *Plethodon* under different temperature ranges. All gradients were cooler toward the bottom of the maze. The maze was uniformly wet. The horizontal line represents the range of temperature over the 4 layers of the maze. Each dot represents the position of a salamander.

moved, the salamanders went back to the wet layers.

Salamanders were seen on the surface almost exclusively at night. Of 815 day time salamander observations, only two were on the surface (0.24%) as compared to 29 surface observations of 774 night salamander observations (3.7%) in the greenhouse mazes. A similar result was noted in the control maze; no surface observations were noted during 301 day time salamander observations as compared to 12 surface observations during 288 night salamander ob-

servations (2.0%). Moisture and temperature gradients seem to affect the occurrences on the surface, but not a significant level.

The mean vertical distributions of day and night were significantly different, although the magnitude of the difference was slight. Salamanders were distributed throughout the mazes both at night and during the day under uniform temperature and moisture. Summing all of the night and day observations in the greenhouse mazes, the mean depth for the day observations was 4.18 in. while that of the night observations was 4.02 in. Thus the night observations averaged 0.16 in. closer to the surface than the day observations. A similar result was noted in the control maze; the night observations averaged 0.6 in. closer to the surface than the day observations. The slightly higher night distribution is almost completely due to surface occurrence during the night observations.

During the November run the wet/dry and dry/wet mazes were inadvertently filled with water. They were drained to the middle of the mazes, and the salamander distributions were noted during the remaining observations. None of the 124 salamander observations were of submerged individuals, although the very tips of the tails were occasionally in the water. The temperature conditions observed were air 16°C, water 12°C; air 11°C, water 12°C; air 12.5°C, water 11.5°C; air 8°C, water 9°C; air 9.5°C, water 8°C; air 14°C, water 10.5°C; and air 4°C, water 4°C. Shaking the mazes did not induce the salamanders to enter the water, but dismantling the mazes did drive them into the water until the disturbance ceased.

DISCUSSION

Litter as part of the total habitat

It has been found in this study that the litter is but a part of the total habitat of these salamanders. While the litter is the most convenient portion of their habitat for study—and therefore where they are most frequently captured—it must not be assumed that such captures are an adequate measure of the ecology of these organisms. The following data support this conclusion:

One hundred nineteen intensive searches of a 70 × 90 ft field plot together with somewhat fewer searches of adjacent and peripheral areas yielded 228 captures of *Plethodon c. cinereus*. Of these, 154 individuals were marked and released. At the conclusion of study the majority of animals captured showed no signs of having been

marked. It may therefore be concluded that the total salamander population is considerably larger than the sample size.

Three lines of evidence indicate that the high number of captures within the plot was due to long-term residents and not immigrants. (1) Measurements of distance moved between recaptures showed very restricted horizontal movements. (2) The direction of these movements and searches of the peripheral areas gave no indication of migration. (3) Salamanders frequently disappeared from the surface and later reappeared under the same object as their original capture, an average of 10 searches later.

Since it appears that the population within the plot exceeded the total number captured on the surface, and since the average number of captures/search was 1.2, only a very small proportion of the population was sampled during rather intensive searches of the plot. This agrees with the findings of Test and Bingham (1948) when they failed to deplete a *Plethodon cinereus* population by the removal of all *Plethodon* found under surface objects. Within experimental field cages, 2% to 32% of the total observations occurred in the top inch of the soil. The proportion found near the surface apparently depended upon temperature, level of the water table, and type of surface shelter available. Within the mazes only a small minority of the observations were made on the surface.

That the surface captures may not be an adequate nor a random sample of the total population has been reported by Test (1955) and is supported by this study. The population sizes within the underground field cages were estimated on the basis of surface captures by a mark and release technique. The surface captures gave an adequate estimate only when underground passageways were not available, as in the trayless cages. In the trayed cages, where underground passageways were available, part of the population remained on the surface while part was never found on the surface. This led to erroneously low estimates. The numerous animal burrows and the disappearance of marked animals indicate that the natural soil provides numerous passageways as do the trayed cages. The non-random movements of *Plethodon* severely limit the use of statistical estimates which assume random mixing. Most authors choose to call the surface captures "abundance," (e.g. Hendrickson 1954, Stebbins 1954) but Gordon (1952) uses the term "visible population." This latter term is more descriptive and less subject to misinterpretation.

It therefore appears that the litter is only a

minor part of the salamander's habitat even under favorable conditions, in contrast to the comment of Vernberg (1953) and the inference of Test (1955) that salamanders use the depths of the soil primarily under unfavorable conditions. Given an opportunity to utilize underground passageways, as in the trayed cages, *Plethodon* penetrated to the full depth of 12 in. Within the mazes, *Plethodon* readily entered darkened burrows. Test (1946) found that the behavior pattern responsible for the well-known tendency for *Plethodon cinereus* to be found under objects is dependent on their negative response to light, but not to dorsal contact. Such a behavior pattern could result in the utilization of burrows as readily as the utilization of superficial shelter objects. Thus the habitat is best described in terms of volume rather than surface area.

The vertical distribution is predictable to some extent, as shown by the responses in the cages and mazes. Additional work along these lines to improve the predictability could yield estimates of total population parameters by measuring soil conditions and observing litter occurrence. This general method should be applicable to any cryptic population that has at least some part of its habitat convenient for study. One caution must be observed: because of the lag effect, shown by the slowness of the return of individuals to areas from which they had previously been driven out by unfavorable conditions, the distribution at a particular time may reflect previous conditions as well as present conditions. Therefore, frequent environmental measurements must be taken.

Seasonal distribution

Captures varied seasonally being high during the spring and autumn and low during the summer. Seasonal changes in captures could be due to seasonal climatic conditions and/or seasonal behavior patterns. The occurrence of more *Plethodon* on the surface of the plaster mazes during the spring and fall indicates that seasonal behavior patterns may exist. This was true both in the greenhouse mazes under semi-natural seasonal conditions, and in the control maze under constant conditions, although not at a statistically significant level. Test (1955) stated that the decrease in the captures of mature females during the summer may be due to their being in nursery chambers. No significant seasonal changes in the mean vertical distributions were found in the mazes.

Temperature

Temperature had a limited effect on the distribution. The highest captures/search were made

as the surface temperatures increased during the spring and as they decreased during the fall. Either the temperatures or the change in temperature may influence surface occurrence. The range of surface temperatures for *Plethodon* captures in the plot was from 5°C to 25°C. Within the underground cages, *Plethodon* were found over approximately the same range, 4°C to 25°C, although temperatures as low as -6°C were sampled. The range here is much wider than that shown for this species by Bogert (1952) of 16°C to 21°C. This wide range is in partial accord with Bogert's conclusion that salamanders do not exercise control over the thermal level of their bodies by their activities and choices of their immediate environment as he has found in lizards. However, his statement that salamanders are insensitive to temperatures within their environment must be modified, for *Plethodon* sharply avoids temperatures below 4°C. The data here are in accord with Vernberg's findings (1953) that *Plethodon cinereus* and *Eurycea bislineata* will avoid air temperatures of 0°C by burrowing into warmer sand. In the mazes, the vertical distribution was markedly influenced by temperature ranges which extended above 18°C; at temperatures above this, the distribution was skewed toward the cooler end. Under the maze conditions the salamanders were sensitive to temperature differences as small as 1.5°C if the temperature was above 18°C. In the cages no temperature avoidance was noted at the higher temperatures up to 25°C, which was the highest temperature sampled. In the field plot captures were made up to 25°C although slightly higher temperatures were sampled, and the distribution of captures was skewed away from the higher temperatures. Thus it appears that the *Plethodon* were more sensitive to temperature under the maze conditions than under field conditions. The complete avoidance of temperatures exceeding 27°C is in keeping with the report (Zweifel 1957) that the maximum lethal temperatures for numerous species of salamanders are between 30° and 36°C.

Moisture

There is particular interest in the moisture relationships of amphibians because they represent a transitional stage between terrestrial and aquatic organisms. It has been shown that at constant temperature, salamanders will lose water through evaporation at a rate inversely related to the relative humidity but will eventually desiccate even in saturated air, so that water in a liquid form is occasionally necessary (Ray 1958, Hall 1922). The water relationships within the soil are therefore of

interest. Within soil cavities, the air will be saturated with water vapor if the soil is wetter than the hygroscopic coefficient (Lutz 1946). Since this was the case in the cage experiments, lowered relative humidities were not studied here; nor could the reactions to soil moisture be studied in the field. The soil within the cages was almost always saturated, and the percentage of water in the soil samples taken from the capture sites is more an indication of high organic content of the soil than of moisture available to salamanders. In the mazes the salamanders avoided dry layers unless the wet layers were warmer than 18°C and the dry layers cooler.

In both the mazes and cages *Plethodon* showed a clear avoidance of standing water. As the water table rose in the cages, the salamanders abandoned the inundated layers. It was noted that high captures/search frequently, but not always, followed heavy rains. It may be that when the soil is saturated, additional rain fills the underground passageways and the salamanders are driven upward.

Diel periodicity

While salamanders appeared on the surface only when it was dark, the vertical distribution within the soil was only very slightly affected by light and dark cycles both in the cages and the mazes. Nor were the number of captures under superficial shelter objects significantly higher at night than during the day in the research plot as might be expected of nocturnal animals. Since salamanders can avoid light by retreating under superficial shelter objects, it is not necessary to retreat deeply into the soil. It appears that the salamanders near the surface may move onto the surface when it is not light, for they are photonegative (Vernberg 1955, Test 1946), but no indications of daily vertical migrations were seen in the plot, the cages, or the mazes.

Comparison of experimental and plot results

It must be concluded that the results of the cage experiments were a poor measure of the plot results. Yet the temperature data of the two areas had almost identical ranges. At least part of this failure was probably due to the location of the cages near the stream, since *Plethodon* tended to be found away from the stream. Had the cages not been so close to the stream where the water table level was the major controlling factor, the results of the cages might have been in better agreement with the plot results. Within the cages, *Plethodon* reacted to environmental conditions and thus gave some measure of the

vertical distribution under these conditions. In a similar manner, the mazes showed that salamanders do react to temperature and moisture gradients in a predictable manner. The extent to which such experimental results can be applied to field interpretations requires additional studies.

Home range

The restricted horizontal movements of marked animals illustrates that they have a restricted home range. Restricted home ranges have been shown for numerous amphibians, *e.g.* *Rana clamitans* (Martoff 1953), *Scaphiopus holbrookii* (Pearson 1955), and *Batrachoseps* (Hendrickson 1954). Since no defense was noted in this study they cannot properly be termed territories.

Hibernation survival

Hibernation survival in the cages was 50% for the winter of 1957 and 0% for the winter of 1958. The 1957 results compare closely with those of Vernberg (1953) of 43% survival. Survival undoubtedly depends upon the severity of the winter, for 1958 was a colder winter with less snow.

Experimental shelter objects

Experimentally placed objects, pine boards, rocks, and tar paper, were found to yield approximately twice as many captures as naturally occurring logs and rocks per foot of cover. One factor relating to this efficiency is the ease of scanning the one square foot under the experimental objects as compared to scanning several square feet under logs, especially at night.

SUMMARY

1. The distribution of *Plethodon c. cinereus* within the soil was studied as a means of interpreting field captures.

2. Three approaches were used: (1) a mark and release method in a field plot for a study of the surface captures of *Plethodon* under natural conditions, (2) underground field cages, in which the vertical distribution could be measured under partially natural conditions, and (3) mazes, in which the vertical distribution could be measured under controlled simulated soil conditions.

3. It was found that *Plethodon* captures (1) varied seasonally, captures occurring more frequently during spring and fall (2) tended to occur away from the stream, and (3) occurred from 5°C to 25°C. Recapture data indicated restricted home ranges.

4. It appears that the litter of the soil is only a minor part of the salamander's habitat even under favorable conditions. With the underground field cages it was found that *Plethodon*

are distributed within the soil, at least to a depth of 12 inches if they are given the opportunity to utilize water-free underground passageways. Those found on the surface or within the first inch of soil were but a small part of the population under plot, cage, and maze conditions. The vertical distribution is affected mostly by water relationships, especially water table level, temperature, and to a limited extent, by light. *Plethodon* avoided inundated soil, but preferred a moist substrate. Within the plot, cages, and mazes, an avoidance of low temperature was found. In the mazes, an avoidance of high temperature was also found. Light had little effect on the vertical distribution within the soil, but did affect exposure on the surface, and thus affected average vertical distribution to a limited extent. Light did not affect the frequency of captures under superficial surface objects in the field plot. A lag was shown in the return of *Plethodon* to areas where they had previously been driven out by unfavorable conditions.

5. Thus a *Plethodon* population reacts toward environmental conditions in a somewhat predictable manner. Additional work along these lines to improve the predictability could yield estimates of total population parameters by measuring soil conditions and observing litter occurrence. This general method should be applicable to any cryptic population that has at least some part of its habitat convenient for study. Numerous environmental measurements must be taken over a period of time since the distribution of the organism may reflect previous conditions as well as present conditions.

6. Hibernation survival depends upon the severity of the winter, 50% of the caged *Plethodon* survived during the winter of 1957 while none survived the winter of 1958 which was colder with less snow.

7. Experimentally-placed shelter objects, pine boards, rocks, and tar paper had approximately twice the efficiency of naturally occurring logs and rocks in yielding salamander captures.

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A POPULATION SURVEY OF RHESUS MONKEYS IN NORTHERN INDIA: II. TRANSPORTATION ROUTES AND FOREST AREAS¹

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This paper presents data on the abundance and population structure of rhesus monkeys (*Macaca mulatta* Zimmerman) observed along roadsides,

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canal banks, railroad rights-of-way, and forest areas of northern India from September, 1959, to June, 1960. A previous paper presented population data on rhesus monkeys in villages, towns, and temples in the same region (Southwick, Beg and Siddiqi 1961). These several types of habitat and survey categories were selected because they represented logical categories in the habitat distribution of rhesus monkeys, and they provided a convenient system of data classification for the

planning and execution of field work. Systematic field surveys of these categories provided coverage of all major rhesus monkey habitats in India.

The objectives of this study were: (1) to determine the most practical method of censusing rhesus monkeys over an extensive area, (2) to obtain data on abundance, distribution, habitat preferences, group sizes, and population composition of rhesus monkeys in northern India, and (3) to estimate trends in the rhesus populations.

Despite the great interest in rhesus monkeys as experimental subjects in biological, medical, and psychological research, practically no extensive studies of the ecology, natural history, or behavior of the rhesus in its natural habitat had been conducted prior to 1959. Except for the limited observations of Nolte (1955) on group sizes, and Prakash (1959) on breeding seasons, no data have been available on such fundamental topics as general abundance, habitat preferences, group sizes, sex and age ratios, reproductive rates, and basic population trends.

This lack of knowledge concerning an important primate species is also surprising in light of the economic, medical, and philosophical significance of the rhesus in India. The rhesus is frequently considered a serious agricultural pest, but estimates of crop damage have been impossible without data on abundance, distribution, and feeding patterns. The rhesus, living in intimate contact with the human population of India, has been recognized as a potentially dangerous reservoir of human disease, but only a few epidemiological surveys have been conducted among natural groups of rhesus (Manson-Bahr 1954, Ruch 1959). The rhesus also possesses an important, although highly variable and confusing, philosophical significance in India. Traditionally associated with Hanuman, the Monkey God, and the Hindu myth of Rama, the rhesus occupies a semi-sacred status among some Hindu groups. All of these features of the rhesus monkey have been mentioned previously (Southwick, Beg and Siddiqi 1961), but they are reiterated here to emphasize some of the unusual ecological and traditional affiliations of the rhesus.

This paper does not attempt to discuss any of these affiliations *per se*. It does, however, present basic population data which might be helpful in evaluating some of the economic, medical, and social aspects of rhesus monkey ecology.

METHODS

The population survey work outlined in this paper was conducted mainly in the state of Uttar Pradesh, with minor excursions into Madhya

Pradesh, Rajasthan, and the Punjab. This area is in the north central portion of the range of the rhesus in India (Figure 1, taken from range descriptions in Pocock 1929, and Prater 1948), and it is commonly considered to be an area of high rhesus abundance. A brief description of the geographical and climatic features of Uttar Pradesh has been presented previously (Southwick, Beg and Siddiqi 1961).



FIG. 1. Approximate range of the rhesus monkey (*Macaca mulatta*) in India. Drawn from the descriptions of Pocock (1929) and Prater (1948).

To permit regional comparisons within Uttar Pradesh, the state was divided into 4 regions: western, central, eastern and southern, and northern (Figure 2). Roadside and railroad surveys were conducted in each region, whereas canal bank surveys were confined to western U.P., and forest surveys were limited to northern U.P.

In each type of survey, we attempted to find as many rhesus groups as possible, and to obtain sex and age counts of the groups whenever possible. Systematic field procedures were adopted for each type of survey to permit quantitative indices of abundance.

The roadside survey consisted of driving along roads in an automobile at an average speed of 20 miles per hour with at least one person other than the driver keeping constant watch for monkeys along the roadside. Only such driving from 7:00 to 11:00 AM and from 3:00 to 6:00 PM was counted in the data. At times other than these, there may have been slightly reduced probabilities of seeing rhesus groups along the roadside. Prior



FIG. 2. Map of Uttar Pradesh, showing regional divisions selected for population surveys.

to 7:00 AM and after 6:00 PM, roadside groups were often out feeding in fields away from the roadside, and during mid-day they were likely to be sleeping in trees along the roadside, particularly during hot weather.

When monkeys were seen, we stopped the car and walked along the roadside to count all individuals in the vicinity. We carried a supply of gram nuts, peanuts or small fruits to feed the monkeys. Most groups came readily to food. In fact they could usually be called in for food by uttering a loud "OH, OH, OH, OH" call which is used by Indian people when feeding the monkeys. Hence, we could be reasonably certain of counting all individuals in a group. In some circumstances it was impossible to count the group—if the individuals were very shy, or widely dispersed, or if the roadside cover was exceptionally dense. We were able, however, to obtain reliable counts on more than half of all groups seen.

The canal bank survey utilized the same procedures driving along the canal access roads on the banks of major irrigation canals, primarily the upper and lower Ganges canals. These roads were frequently gated and were not open to vehicular traffic, but we obtained excellent cooperation from engineers and gatekeepers to unlock the gates for us.

The railroad survey was done on local trains which stopped frequently, thereby permitting

enough time at most stations to jump off the train and make a quick inspection of the railway platforms and station yards for the presence of monkeys. Only such inspections made from 7:00 to 11:00 AM and from 3:00 to 6:00 PM were considered in the data. Due to the habit of rhesus monkeys to sit atop buildings and sheds, and to be fairly active during the hours listed above, it was usually easy to spot rhesus in railroad stations. Of course, they could be missed if they had moved into a neighboring bazaar, or if they might all be behind some building. Obviously none of these types of survey was without observational error.

The forest survey was a brief investigation conducted during a 3-week period in May, 1960, in the forests of northern U.P. Two centers were selected for study, Corbett National Park, north of Moradabad, and Naini Tal, north of Bareilly. At each center, 3 different forest blocks were selected representing different forest types. In each forest block, one or more areas of approximately one square mile were chosen. These areas were usually delimited by footpaths or fire lanes. We walked slowly around these areas, pausing for 10 minutes every 200 to 300 yards. One transect was then taken through the center of the area. Since this work was done at the driest time of the year, any movement of large animals in the forest could be heard for a distance of approximately 200 yards. This was particularly true of monkeys which could be detected from some distance by sounds of movement or vocalization.

The forest areas were selected with local advice as to the areas where monkeys would be most abundant. All forest areas surveyed contained available water or were adjacent to streams or rivers. In Corbett National Park, 4 square miles were mixed deciduous forest (Champion 1936), one square mile was pure sal (*Shorea robusta* Gaertn.) forest, and one square mile was pure sheesham (*Dalbergia sissoo* Roxb.) forest. All were at an altitude of 1000 to 2000 feet in the Ramganga River valley. At Naini Tal, 2 square miles were oak and pine forest at 4000 to 5000 feet, one square mile was oak and pine at 5000 to 6000 square feet, and one square mile was oak, pine and fir forest at 6000 to 7000 feet.

In all types of survey, the individuals observed were placed into one of 4 categories: adult males, adult females, infants, and juveniles. Infants were identified as young which were generally dependent upon the mother, were not yet weaned, and which were usually carried by the mother during group progression. Infants were definitely less than 4 pounds in body weight, and were judged

TABLE I. Population survey of rhesus monkeys in northern India: Incidence and group structures ($\bar{X} \pm \text{s.e.}$)

Type of survey	Miles trav.	Groups seen	Miles per group	Groups counted	Average group size	ADULTS		SUBADULTS	
						♂♂	♀♀	I I	J J
Roadside.....	4642	406	11.2	230	15.1±0.6	3.5±0.1	6.9±0.3	3.8±0.2	0.9±0.2
Canal Bank.....	200	37	5.4	26	19.0±2.0	4.4±0.4	8.4±0.9	5.5±0.6	0.7±0.3
Railroad.....	2730	84	32.5	34	11.3±1.4	2.6±0.4	5.0±0.7	2.7±0.4	1.0±0.2
Forest.....	10 sq. mi.	7	—	5	49.8±5.8	5.6±0.7	19.2±1.7	11.4±0.7	13.6±2.9

to be less than one year old. Such individuals frequently moved on their own some distance from the mother during play or feeding, but most of the time they remained closely associated with her.

Juveniles were identified as young which were largely independent of the mother, definitely weaned, and more than 4 pounds in body weight. They were judged to be more than one year of age, and less than 4. The differences between infants and juveniles, as here defined, were usually definite. Occasionally borderline individuals were seen; these were watched closely and an arbitrary judgment was made. If the individual was seen to ride upon the female, or was seen to nurse successfully, it was classified as an infant.

Juveniles were distinguished from the adults by their smaller size and lack of red sexual skin. Both of these characteristics are highly variable, however, and subjective judgments were necessary on many occasions.

The division of this population survey into distinct categories obviously led to certain problems of classification. For example, in cases where villages were located along roadsides, a group of monkeys living in the vicinity might be considered either a village group or a roadside group. Monkeys living at points where road bridges crossed canals could be considered either roadside groups or canal bank groups. These problems of classification were handled by determining which locale represented the usual and most frequent habitation of the group. The home ranges of the monkeys were often very restricted; the main sleeping and feeding areas quite specific. This usually warranted the placement of the group into one category. In a few cases where 2 habitat categories were apparently utilized in an equivalent manner, an arbitrary placement was made depending upon how or where the group was first seen.

RESULTS

During 9 months of field survey, 534 groups of rhesus monkeys were seen in 4 habitat categories:

406 in roadside habitats, 37 along canal banks, 84 in railroad stations and along railroad rights-of-way, and 7 in forest areas. Concurrently, 89 rhesus groups were seen in villages and towns, and 15 in temples (Southwick, Beg and Siddiqui 1961). This does not, however, provide an accurate concept of the relative importance of these habitat categories in the total pattern of population distribution. It merely gives some indication of the relative ease of finding rhesus monkeys in these various types of habitats.

Reliable counts were obtained on 295 groups in the 4 categories under consideration, involving a total of 4632 individuals. The average group size was 15.7 individuals, composed of 3.5 adult males, 7.1 adult females, 4.0 infants, and 1.1 juveniles. The average group size of 104 village, town and temple groups previously reported was 22.8 individuals, composed of 4.5 adult males, 9.3 adult females, 5.8 infants, and 3.2 juveniles. There were, however, significant differences in group sizes and compositions between specific categories (Table I; Figure 3).

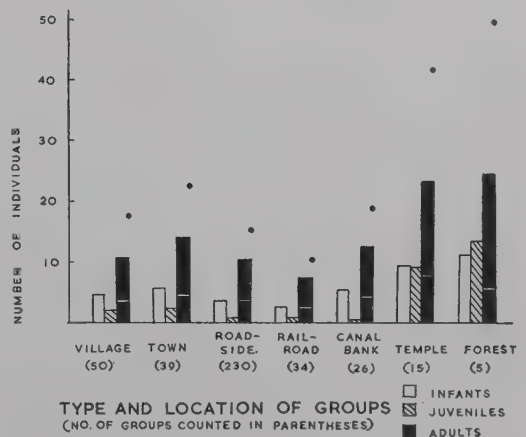


FIG. 3. Group sizes and compositions of rhesus groups in different habitat categories. Round dots represent total group sizes; lower portions of solid bars represent adult males, upper portions of solid bars, adult females.

TABLE II. Incidence and group structures of rhesus monkeys observed in roadside survey of northern India

Location	Miles	Groups seen	Miles per group	Groups counted	Average group size	ADULTS		SUBADULTS	
						♂♂	♀♀	I I	J J
Western U.P.....	2655	191	13.9	65	16.2±1.3	3.6±0.3	6.9±0.6	4.6±0.4	1.1±0.3
Central U.P.....	538	79	6.8	63	14.2±1.1	3.6±0.3	7.1±0.4	3.2±0.4	0.3±0.2
Eastern and Southern U.P.	626	72	8.7	62	12.4±0.7	2.9±0.2	6.0±0.4	2.9±0.3	0.5±0.2
Northern U.P.....	542	57	9.5	36	19.3±1.9	3.7±0.3	8.2±0.8	5.2±0.5	2.2±0.6
Central M.P.....	281	7	40.1	4	18.5±7.0	3.5±0.9	11.0±4.0	1.8±1.0	2.2±1.1
Total.....	4642	406	11.2	230	15.1±0.6	3.5±0.1	6.9±0.3	3.8±0.2	0.9±0.2

Roadside survey

In a total of 4642 miles driven under the conditions specified, 406 groups of rhesus monkeys were seen, an average of one group every 11.2 miles. The region of greatest abundance for roadside monkeys was central U.P., where a rhesus group was seen for each 6.8 miles driven (Table II). Eastern U.P. showed the next highest incidence of roadside monkeys with one group per 8.7 miles. Although northern U.P. also showed a fairly high incidence of roadside groups (one group per 9.5 miles), this was due primarily to a high incidence in one locality: the Pilibhit-Tanakpur area bordering Nepal. Here one rhesus group was seen per 4.8 miles, whereas most of the northern U.P. showed only one group per 13 to 17 miles.

Within central and eastern U.P., the specific area with the greatest abundance of roadside monkeys extended from Shahjahanpur through Lucknow in central U.P., to Faizabad and Gorakhpur in eastern U.P. Major roads between these cities revealed a total of 94 groups in 388 miles, an average of one group every 4.1 miles. One locality of outstandingly high concentration of roadside groups occurred between Ajodhya and Faizabad in eastern U.P. where 17 groups were seen in 5 miles.

In western U.P. around Aligarh and Agra, and in southern U.P. around Allahabad, roadside groups were seen no more frequently than every 12 to 15 miles on the average. Throughout all of U.P. the area of least abundance of roadside monkeys was around Delhi, where only one group was seen per 29 miles traveled. This included neighboring sections of Rajasthan and the Punjab.

In the entire roadside survey, the area of least abundance of roadside groups was central Madhya Pradesh, around Jubbulpore, where only 7 groups were seen in 281 miles, an average of one group every 40 miles. For reasons mentioned later, however, this sample was probably not comparable with most of the U.P. survey.

To evaluate the reliability of roadside survey

methods, one section of typical roadside 104 miles in length from Delhi to Hathras was selected. Frequent surveys on this road indicated that 14 groups of rhesus monkeys lived along the roadside. During 10 repetitions of the trip under similar conditions, the lowest count of groups seen during a single trip was 3, the highest count was 11, and the average was 7 groups per trip. On no single trip were all groups seen. This suggests that an average roadside survey trip on the plains, under standard conditions, reveals about 50% of the total number of groups which inhabit the roadside. It is probable, however, that roadside survey was less effective in hilly and forested areas of northern U.P. and central M.P. (see Discussion section).

The average size of 230 roadside groups counted was 15.1 individuals, composed of 3.5 adult males, 6.9 adult females, 3.8 infants, and 0.9 juveniles (Table II).

Canal bank survey

During a total of 200 miles driven on canal banks in western U.P., 37 groups of rhesus were seen, an average of one group every 5.4 miles. Hence, this sample of canal banks showed twice as many rhesus groups per unit distance as the overall sample of roadside survey ($\chi^2 = 2.8569$; $P < 0.10$).

The average size of 26 canal bank groups counted was 19.0 individuals, composed of 4.4 adult males, 8.4 adult females, 5.5 infants, and 0.7 juveniles. This larger group size is not statistically greater ($\chi^2 = 0.8006$; $P > 0.30$) than that of roadside groups, but it does support the idea that canal banks are more favorable habitats than roadsides.

Railroad survey

In 2730 miles of railroad travel, 84 rhesus groups were seen, an average of one group every 32.5 miles. The regions of greatest abundance of railroad groups were central and northern U.P., where one group was seen per 20 to 22

TABLE III. Incidence and group structures of rhesus monkeys observed in railroad survey of northern India

Location	Miles	Groups seen	Miles per group	Groups counted	Average group size	ADULTS		SUBADULTS	
						♂♂	♀♀	I I	J J
Western U.P.....	1333	29	46.0	7	11.0±1.1	2.3±0.2	4.4±0.6	2.6±0.3	1.7±0.3
Central U.P.....	613	30	20.4	7	9.1±1.3	2.2±0.4	4.2±0.5	1.9±0.3	0.8±0.2
Eastern and Southern U.P.	582	16	36.4	13	12.4±1.8	3.2±0.5	5.9±0.7	3.1±0.7	0.2±0.2
Northern U.P.....	202	9	22.4	7	15.6±4.3	3.0±0.6	6.1±1.8	4.0±1.2	2.4±0.8
Total.....	2730	84	32.5	34	11.3±1.4	2.6±0.4	5.0±0.7	2.7±0.5	1.0±0.2

miles traveled (Table III). The area of least abundance of railroad groups was western U.P., where one group was seen per 46 miles.

Of the 84 groups seen, 50 were in railroad stations. In all, 443 railroad stations were visited; hence, rhesus groups were observed in 11% of these.

Of 34 groups counted in railroad stations, the average size was 11.3 individuals, composed of 2.6 adult males, 5.0 adult females, 2.7 infants, 1.0 juveniles. This average group size is not statistically distinct from that of roadsides ($\chi^2 = 0.7517$; $P > 0.30$), but it approaches statistical distinction from canal bank groups ($\chi^2 = 3.040$; $P < 0.10$).

Forest survey

In forested areas of northern U.P., rhesus monkeys were found in both mixed deciduous and mixed coniferous forests up to altitudes of 6,000 feet.

In 10 square miles of forest area surveyed, representing 5 distinct forest types, 7 groups of rhesus were found. Six of these were found in 3 square miles of mixed deciduous forests of Corbett National Park. One group was found in a pine-oak forest near Naini Tal. Rhesus groups were not found in 5 of the 10 square miles surveyed, nor were they found in 3 of the 5 forest types surveyed (Table IV).

During the same survey, 10 groups of langurs (*Presbytis entellus*) were seen in 7 of the square-mile areas surveyed, representing 4 of the forest types. Hence, langurs were more abundant and more widely distributed than the rhesus in the forests sampled.

The abundance of rhesus monkeys in the mixed deciduous forest of Corbett Park probably represented a seasonal concentration. At the height of the dry season, the monkeys were definitely concentrated near available water, and all of the forest areas studied in this survey contained available water or were adjacent to rivers. All of the forest work in Corbett Park was done along the Ramganga River. There were extensive forest

areas farther up the slopes which were totally devoid of surface water, and were probably devoid of monkeys. This statement is based upon our own observations, and also upon the opinions of the Corbett Park Forest Officers.

The average group size of forest monkeys was the largest observed in this study: a total of 49.8 individuals, composed of 5.6 adult males, 19.2 adult females, 11.4 infants, and 13.6 juveniles. This average is probably an underestimate of true group size in forest areas. Rhesus groups in the forest were very difficult to count. The animals were wild and shy and often spread out over an area 100 or 200 yards in diameter. They could only be counted when seen crossing a dry stream bed, a forest road, or some similar opening. The counts obtained suggest that some adult males were missed, quite possibly the peripheral males characteristic of most rhesus groups.

Forest groups of rhesus also had good percentages of juveniles (27.3%). In this regard they were significantly different from roadside, canal bank, and railroad groups, but were similar to temple groups previously described (Southwick, Beg, and Siddiqi 1961).

Population composition

The percentages of each sex and age group in the population samples of different habitat categories are shown in Table V. Data from villages, towns and temples are also included in this table.

Of the total 7,003 individuals counted in all categories, 21.4% were adult males, 43.6% were adult females, 25.5% were infants, and 9.5% were juveniles. The adult sex ratio was 30.7% male; the infant/adult-female ratio was 58.4%, and 35% of the total population was subadult (Table V). Some significant differences in population composition between different survey categories did occur, however.

The percentages of adult males in groups of different categories were usually 19% to 23%, except in forest groups where it was only 11.2%. This probably represents a failure to count peripheral males in dense forest cover.

TABLE IV. Forest survey of rhesus monkeys in northern Uttar Pradesh: Incidence & group structures

Location	Forest type	Altitude (feet)	Man-hours obs.	Sq. mi.	Langur groups seen	Rhesus groups seen	Rhesus group size	ADULTS		SUB-ADULTS	
								♂ ♂	♀ ♀	I I	J J
Corbett Nat. Park . . Dhikala area	tropical mixed deciduous	1000-2000	20	1	1	3	60 32 ca. 45	6 4 —	24 14 —	14 9 —	16 5 —
Corbett Nat. Park . . Dhikala area	"	"	8	1	0	0	—	—	—	—	—
Corbett Nat. Park . . Dhikala-Sarupduli area	"	"	12	1	1	2	40 ca. 40	4 —	16 —	11 —	9 —
Corbett Nat. Park . . Sarupduli area	"	"	10	1	2	1	49	6	21	12	10
Corbett Nat. Park . . Dhikala area	sal	"	10	1	0	0	—	—	—	—	—
Corbett Nat. Park . . Dhikala area	sheesham	"	8	1	1	0	—	—	—	—	—
Naini Tal Bhowali area	pine-oak	4000-5000	12	2	1	1	68	8	21	11	28
Naini Tal Kale Khan area	"	5000-6000	18	1	2	0	—	—	—	—	—
Naini Tal Malli Tal area	pine, oak, fir	6000-7000	24	1	2	0	—	—	—	—	—
Totals				10	10	7	49.8 ±5.8	5.6 ±0.7	19.2 ±1.7	11.4 ±0.7	13.6 ±2.9

TABLE V. Population compositions of rhesus monkeys in different habitat categories

Habitat	No. of monkeys counted	♂ ♂	♀ ♀	II	JJ	♂ ♂/Ad.	II/♀ ♀	Young/Tot.
Roadsides	3469	22.8%	46.0%	25.3%	5.9%	33.2	55.1	31.2
Canal Banks	494	22.3	43.9	29.2	3.6	34.6	66.4	32.8
Railroads	420	23.1	43.8	24.0	9.1	34.5	54.9	33.1
Villages	869	20.4	41.6	26.6	11.4	32.8	63.8	38.0
Towns	873	19.8	43.2	26.4	10.5	31.2	60.8	36.9
Temples	629	18.7	36.2	22.7	22.3	34.1	62.7	45.0
Forests	249	11.2	38.6	22.9	27.3	22.6	59.4	50.2
Totals	7003	21.4%	43.6%	25.5%	9.5%	30.7%	58.4%	35.0%

The adult sex ratio normally varied from 31% to 34% males in all survey categories, except in forest groups where it was only 22.6%.

The percentages of females, infants, and the infant/adult-female ratio was quite similar in all types of groups. Adult females made up 36% to 46% of the total populations, infants comprised 23% to 29%, and the infant/adult-female ratio varied from 55% to 66%.

The greatest variation in population composition occurred in the percentages of juveniles. Roadside and canal bank groups had less than 6% juveniles; railroad, village and town groups had

approximately 10%; whereas temple and forest groups had 22% and 27% juveniles respectively. If temple and forest groups are considered normal age-structured groups, all other groups surveyed had significantly deficient percentages of juveniles ($\chi^2 = 698.904$; $P < 0.01$).

Seasonal patterns of reproduction

Newborn young were seen primarily in April and May, and a few were also observed in September. The spring months, however, represented a very prominent peak in births (Figure 4). Of 343 adult females observed in 32 groups in April

and May of 1960, 137 (37%) had infants less than one month of age. If all of these groups could have been observed in the latter part of May, undoubtedly a higher percentage of newborn infants would have been seen. In contrast to this, of a total of 622 adult females seen in September and October, only 7 (1.1%) had newborn infants, and of 2092 adult females seen from November to March, none had newborn infants.

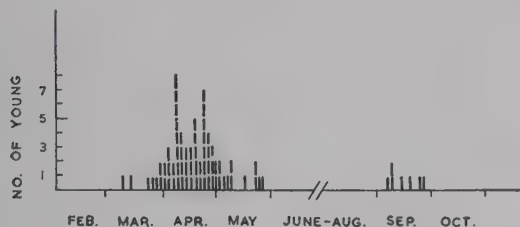


FIG. 4. Estimated birth dates of 73 infant rhesus observed at less than 10 days of age. Each vertical line segment represents one individual.

A similar seasonal pattern of births has been observed by Prakash (1958). In 3 large groups of rhesus near Jaipur in northern India, most births occurred from March 25 to May 7, but a few were observed from September 28 to October 8. None were seen at other times of the year.

This well-marked seasonal pattern of births would normally be expected to have a marked influence on the age ratios observed in different seasons. However, most of the rhesus groups described in this report were subjected to intensive trapping pressure directed against infants and juveniles, so that infants were frequently trapped and removed at the time of weaning, which normally occurred as soon as the younger sibling was born. From the observational standpoint, therefore, the broad categories of age ratios used in this study appeared to be seasonally stable. Two possible exceptions were the temple and forest groups. The subject of trapping removal has been discussed previously (Southwick, Beg and Siddiqi 1961).

DISCUSSION

General abundance and regional distribution

Although this survey, and the one previously reported, attempted to cover all major rhesus monkey habitats in the state of Uttar Pradesh, it did not provide sufficient data to offer an accurate scientific estimate of total rhesus abundance in U.P. We feel, however, that rhesus monkeys are less abundant than is commonly thought, and for this reason we are willing to express a guess concerning the total rhesus population of U.P. Whereas we were frequently told by responsible

zoologists and government administrators in India that the total rhesus population of U.P. was currently between 10 and 20 million, we feel that slightly less than one million is a more realistic figure. Table VI presents the basis of this guess. There is some basis for the estimates of roadsides, canal banks, railroads, villages, and small or medium towns, but the estimates for large towns, cities, temples and forest areas involve pure guesswork. It is inconceivable to us, however, that the rhesus population of U.P. would greatly exceed one million. In 9 months of intensive field work, we saw fewer than 12,000 rhesus monkeys.

Concerning the pattern of regional abundance, central and eastern U.P. had the greatest numbers of roadside monkeys, specifically the areas around Lucknow, Faizabad and Gorakhpur where one group was observed every 3 or 4 miles on the average. We attribute this to more favorable roadside habitat throughout central and eastern U.P. than in the other regions of U.P. There is a greater abundance of roadside trees, primarily banyan (*Ficus bengalensis* L.), neem (*Melia azadirachta* L.), mango (*Mangifera indica* L.), and other food and shelter trees favored by monkeys (Southwick, Beg and Siddiqi 1961).

Eastern U.P. also showed the highest incidence of village monkeys, and this was attributed, in part, to the greater abundance of preferred trees in the eastern region.

In the railroad survey, the regions of greatest abundance were central and northern U.P., specifically the areas around Lucknow, Faizabad, Laksar and Dehra Dun. In all of these areas the appearance of the habitat in terms of tree cover and available water supplies was quite favorable.

Other areas of high rhesus abundance were the "terai" (tarai) and "bhabar" of northern U.P. The terai is a narrow bank of lowland, marshy jungle between the plains and the Himalayan foothills. The bhabar is an adjacent band of rocky, hilly terrain covered by scrub forest and jungle at the base of the foothills. The 2 types of terrain are frequently interspersed, and together they form a belt 20 to 50 miles in width running most of the length of the Himalayan chain. Typical terai and bhabar country occurs in the vicinities of Dehra Dun, Corbett National Park, Haldwani, and Tanakpur. Rhesus monkeys were abundant in these regions as evidenced by the Dehra Dun village survey, the Corbett Park forest survey, and the Tanakpur road survey.

Habitat distribution

Villages and towns represented the most important habitat categories in this survey, possess-

TABLE VI. Hypothetical estimate of total rhesus monkey population in Uttar Pradesh

Habitat	Rhesus population estimate	Percent of total population	Basis of estimate	Calculation
Roadsides	48,000	6%	(total mileage of roads in U.P.)($\bar{x}$) miles per group in roadside survey	(35,851)(15.1) 11.2
Canal Banks	25,000	3	total mileage of large canals in U.P.)($\bar{x}$) miles per group in canal bank survey	(7,236)(19.0) 5.4
Railroads	4,000	0.5	total mileage of railways in U.P.)($\bar{x}$) miles per group in RR survey	(10,000)(11.4) 32.5
Villages	372,000	46	(total no. of villages in U.P.)(I)(G)($\bar{x}$)	(108,941)(.157)(1.25)(17.4)
Towns (small and medium)	133,000	17	(total no. of sm. and med. towns in U.P.)(I)(G)($\bar{x}$)	(3,104)(.688)(2.78)(22.4)
Large Towns and Cities	100,000	12.5	pure guess	
Temples	20,000	2.5	pure guess	
Forests	100,000	12.5	(Sq. mi. of forest in U.P.)(I)($\bar{x}$)(c.f.)	(15,877)(.7)(49.8)(.20)
Total	802,000			

 $\bar{x}$ = average group size.

I = Incidence of rhesus groups in villages, towns, and forest survey areas.

G = Average number of groups per village or town with resident monkeys.

c.f. = Correction factor for dry season concentration.

ing probably more than half of all the rhesus monkeys in U.P. (Table VI). These small communities afford ideal physical habitat for rhesus monkeys: large trees for cover and food, buildings and walls for shelter from duststorms and monsoon rains, abundant food supplies in fields and gardens around the village, and available water in wells, irrigation ditches, and ponds.

The major disadvantage of the village and town habitat for monkeys is frequent molestation from people. Rhesus monkeys exist in villages and towns only by the tolerance and consent of the people. For centuries this tolerance has been maintained by social tradition and religious custom. Rhesus monkeys have been permitted to live in villages and towns, and to feed upon agricultural crops. Currently, social traditions and customs in India are undergoing rapid change, and the attitudes of tolerance toward monkeys are also changing. Many villagers told us that they could no longer afford to have monkeys in their villages. Hence, monkeys in villages and towns were being trapped, driven away and even killed, because they were competing in a direct and obvious way with the villagers for food.

Forest areas of northern U.P. probably represented the 2nd most important habitat category in this survey in terms of total population distribution. Rhesus were found most abundantly in the tropical mixed deciduous forests of the terai and bhabar. These dense, secondary forests afford excellent cover and adequate natural food (leaves and fruits of *Ficus bengalensis*, *Bauhinia variegata*, etc., see Champion 1936). Within the same

areas, pure stand forests of sal (*Shorea robusta*) and sheesham (*Dalbergia sissoo*) were less favored habitats. These latter forest types are economically most productive, so there is a conflict between productive forest use for human purposes, and monkey abundance.

Water supplies in the terai are abundant during and after the monsoon, but as the dry season progresses, most streams become dry and the monkey population becomes concentrated along major watercourses. This, we feel, is the explanation of the high rhesus abundance found in Corbett National Park, along the valley of the Ramganga River.

Most of the terai and bhabar occupies altitudes around 1,000 feet. In the true Himalayan foothills (3,000 to 10,000 feet), rhesus monkeys were much less abundant. During 2 weeks in the foothills around Naini Tal, Bhowali, and Ranikhet, we found only 2 groups, one in a pine-oak forest at 5,000 to 6,000 feet, and one inhabiting the garbage dump at Naini Tal at an altitude of 6,500 feet.

Roadside and canal bank habitats contained a relatively much smaller segment of the total rhesus population (Table VI), but definitely a more conspicuous segment. Both roadsides and canal banks frequently have rows of large trees, providing food and cover for monkeys, and neighboring fields of agricultural crops. The obvious advantage of canal banks is the abundance of water. Along roadsides, monkeys were usually limited to places where irrigation ditches ran along the road. The dry season in northern India

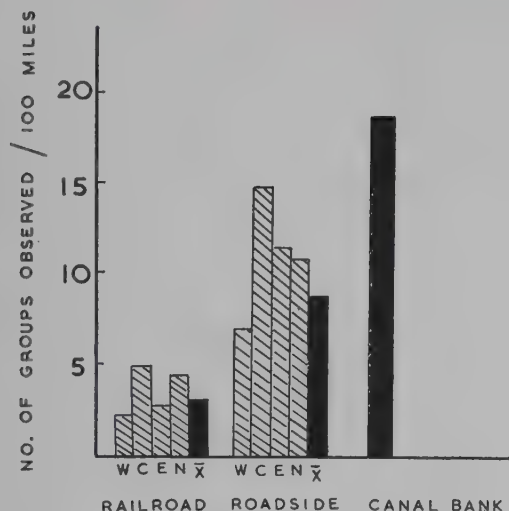


FIG. 5. Average numbers of rhesus groups observed per 100 miles of railroad, roadside and canal bank survey. Solid black bars represent averages for all of U.P.; W represents western U.P.; C, central U.P.; E, eastern and southern U.P.; N, northern U.P.

extends 9 months; water is therefore a critical factor determining monkey distribution.

Both roadsides and canal banks are public property in India, and in a sense, the monkeys are also public property. Living within the public domain, the monkeys are not so obviously in direct competition with any one village for food. When the monkeys ventured into neighboring fields, they were frequently driven back by "chawkidars" guarding the fields, and they retreated again to the roadsides where they were relatively free from molestation.

Temple and railroad station habitats contained minor segments of the total rhesus population, but probably the most stable segments. Here the monkeys also exist as "public property" within the public domain. When the monkeys ventured from these specific habitats into surrounding bazaars or residential areas, they were often chased and driven back by shopkeepers and dwellers. In this respect, temples, railway stations, roadsides and canal banks all represent "refugia" where the monkeys are relatively free from constant molestation, and where they are also fed.

Within these "refugia" rhesus monkeys are a source of entertainment and amusement for the people. Along roadsides and canal banks, passerbys often stop, rest, and feed the monkeys. We have frequently seen busses stop along roadsides, passengers descend to feed a group of monkeys, and then return to the waiting bus to continue

their journey. In temples and railway stations, rhesus monkeys are even more lavishly fed. Many people have a daily routine of coming to feed the monkeys. They apparently do it for amusement, or for an outing with children. Occasionally, they appeared to do it in a spirit of worship.

Temples and railway stations are also significant habitats from other standpoints. They offer the most intimate contacts between monkeys and large numbers of itinerant people of any habitat in India. Infectious diseases reserovired in rhesus monkeys which might be passed to human beings could spread more rapidly across India via temple groups and railway station groups than by any other type of groups.

No specific survey of rhesus monkeys in large towns and cities was attempted in this study. There are 15 cities in U.P. with populations of more than 100,000 people, and numerous large towns with populations from 15,000 to 100,000. Probably all of these have some rhesus monkeys present; we were able to find rhesus groups in all major cities except Allahabad.

In large towns and cities, rhesus groups were usually associated with temples, railway stations, roadsides leading into the cities, or bazaars. Hence, this survey has included many city groups under these categories. Rhesus groups in bazaars were common, but were exceptionally difficult to count and study. Monkeys were frequently seen on rooftops and parapets, but they often disappeared behind buildings and walls in the course of their normal movements. It was virtually impossible to count them in the crowded conditions of bazaars.

Rhesus groups were rarely seen in parks, gardens, civil lines (middle and upper class residential areas), or cantonments (areas of military or governmental buildings). There were, of course, exceptions. In New Delhi, a group of rhesus monkeys inhabit lawns around governmental buildings, and for years they have avoided all attempts to trap them. Also in New Delhi, a large rhesus group inhabit an upper class residential area within a few hundred yards of the Ashoka Hotel, one of India's most modern luxury hotels. Usually, however, there have been trapping campaigns to remove rhesus monkeys from the more prosperous sections of most cities.

Population trends

We believe that the rhesus populations of northern India are declining for at least 3 reasons: (1) changing attitudes of the villagers of India toward rhesus monkeys, (2) trapping removal of

juveniles for the export trade, (3) changing patterns of land use.

The changing attitudes of Indian villagers were apparent in our conversations and interviews with village people (Southwick, Beg and Siddiqi 1961). As a part of the rapid social changes, most villagers are no longer tolerant of extensive crop depredations by rhesus monkeys.

The trapping removal of juvenile rhesus is intensive throughout the range of the rhesus in India. The numbers of juveniles being exported from New Delhi during our stay in India averaged 14,000 per month. This, we feel, is the main explanation for the deficient numbers of juveniles in all groups except temple groups and forest groups. The age ratios indicate that the breeding stocks are not being replaced. Hence, we would predict a considerably more precipitous decline in the rhesus populations within 8 to 10 years when most of the existing adult population has died off. We do not, by any means, expect extermination of the natural rhesus populations in India. We feel that rhesus will continue to exist in forest areas, temple grounds and other protected sites, and probably in slum areas of cities for the foreseeable future.

A 3rd set of factors which undoubtedly influence rhesus populations is changing patterns of land use. We cannot offer quantitative documentation, but we feel that roadside habitats in India are deteriorating. Magnificent stands of roadside trees are being cut at a greater rate than they are being replaced. An interesting, but somewhat tragic, succession of cutting can be seen. Many roadside trees, especially the neem, are intensively pruned by goatherds to provide green leaf fodder for their goats. After many years of over-pruning, the trees die, and woodcutters come in to complete the task. In a definite ecological sense, the goats, with human assistance, are successfully competing against the monkeys for the leaves of neem trees. The intense pressure for lumber and firewood is also seen in the cutting of orchard groves. Within 20 miles of Aligarh, 2 fine mango groves, both of which contained groups of rhesus monkeys, were cut to the ground during our stay in Aligarh. The living trees were chopped up for wood. The rhesus habitats were entirely destroyed. The groups dispersed and were last seen wandering many miles from their original mango groves apparently in search of new habitat.

In the forest of northern U.P., a different type of land use practice has had a deleterious effect upon rhesus habitat. In certain areas along the Ramganga River valley we saw mixed de-

ciduous jungle being cleared and converted into pure stands of sal and sheesham forest. Sal and sheesham are both high quality lumber trees, and economically it is highly desirable to convert rather useless scrub jungle into more productive sal and sheesham forests. With the continued economic development of India, therefore, we would expect more and more forest management programs, and the conversion of scrub jungle into timber producing stands of sal and sheesham. Our forest survey indicated, however, that scrub forest is definitely more favorable rhesus habitat than pure stands. Hence, there will probably be continued shrinkage of jungle habitat throughout the Himalayan foothill area.

Comments on survey methods and suggestions for further research

The rhesus population of northern India affords outstanding opportunities for additional research in primate ecology. There is a need for more work on abundance, distribution, population trends, reproductive rates, patterns of movement, and social behavior, not only in Uttar Pradesh, but also in other states, particularly Bihar, Bengal, Assam, and Madhya Pradesh. There has been essentially no published studies on food habits, growth, maturation, physical condition, disease relationships, and longevity of wild rhesus monkeys in India.

To obtain more complete data on abundance, distribution and population trends, we feel that additional population survey work should concentrate on 4 of the 6 categories attempted in this study: village and town survey, forest survey, roadside survey, and canal bank survey.

Village survey proved to be a tedious and relatively unproductive task, but an important one since village monkeys represented the largest portion of the total rhesus population in U.P. A routine working day, in which we could inspect 6 to 8 villages frequently yielded no monkeys at all. A working period of 2 weeks, however, could cover 75 to 100 villages and obtain a good picture of the incidence of village monkeys within a particular area. Since the incidence of village monkeys was already low in some areas, it will require rather time-consuming effort to detect significant population trends in village monkeys. One of the most productive regions for additional village survey would be eastern U.P.

Forest groups were likewise difficult to survey. A routine working day could adequately survey one to 2 square miles of forest land, depending upon the terrain and forest density. Although there is relatively little forest land in U.P., forest

groups occupy an increasingly important segment of the total population. Additional work on forest monkeys should be concentrated in the terai and bhavar.

Roadside and canal bank surveys provided the most efficient field technique for obtaining large numbers of group counts (Figure 5). In the open flat country of the Gangetic plain, where roads are often elevated above the surrounding fields, and where the largest trees of the landscape are openly spaced along the roadside, the probability of seeing monkeys is sufficiently high to make automobile survey an accurate census procedure. A working routine of 75 to 125 miles per day, obtaining counts of 10 to 20 groups was quite feasible on most roads. On canal banks a normal working day could cover only 50 to 75 miles because of frequent delay at locked gates.

Roadside survey was not effective in hilly, mountainous, or forested areas. In such terrain the probability of seeing monkeys from the roadside was greatly reduced. Our roadside survey in the hills of central Madhya Pradesh, for example, which revealed only 7 groups in 281 miles, was probably not a good index of rhesus monkeys in this area. In the hills and mountains of northern U.P., the roadside data were likewise probably inaccurate. In Corbett Park, merely driving down forest roads often revealed no monkeys at all on some trips, but quite a few on other trips. The only effective way of finding monkeys in forest areas was by slow, systematic hiking and waiting.

We feel that temple survey and railroad survey are not necessary in a study of general population trends since these habitats contained a very small portion of the total rhesus population. Both are important habitats to study in epidemiological surveys, however. Temple habitats also provide excellent locations for the study of social behavior.

SUMMARY

During 9 months of field survey in northern India, conducted from September, 1959 to June, 1960, 534 groups of rhesus monkeys were seen in roadside, canal bank, railroad, and forest habitats. During the same period, 104 rhesus groups were seen in village, town and temple habitats.

The average group sizes observed were: 15.1 individuals for roadside groups; 19.0 for canal bank groups; 11.3 for railroad groups; 49.8 for forest groups; 17.4 for village groups; 22.4 for town groups; and for 41.9 for temple groups.

Counts obtained on 399 groups in all habitat categories revealed an overall average group size

of 17.6 individuals, composed of 3.7 adult males, 7.7 adult females, 4.5 infants, and 1.7 juveniles.

Rhesus monkeys were most abundant in central and eastern U.P. in the areas around Shahjahanpur, Lucknow, Faizabad, and Gorakhpur; and also in the "terai" and "bhavar" of northern U.P. (hilly and swampy jungle terrain). Monkeys were considerably less abundant in western U.P., southern U.P. and in the mountains of northern U.P.

In 4642 miles of roadside survey, 406 groups of rhesus were seen, an average of one group every 11.2 miles. From Shahjahanpur to Lucknow in central U.P., and on to Faizabad and Gorakhpur in eastern U.P., rhesus groups occurred on the average of every 4.1 miles. The greatest concentration of roadside groups was observed between Ajodhya and Faizabad, where 17 groups were seen in 5 miles.

Repeated roadside survey between Delhi and Hathras indicated that average roadside survey, under standard conditions revealed about 50% of all roadside groups.

In 200 miles driven on canal banks in western U.P., 37 groups of rhesus were seen, an average of one group every 5.4 miles.

In 2730 miles of railroad survey, 84 rhesus groups were seen, an average of one group every 32.5 miles. A total of 443 railroad stations were visited; rhesus groups were observed in 50 (11%).

A survey of 10, one-square-mile areas of forest land in northern U.P. revealed 7 groups of rhesus in 4 of the areas. Six of these groups were found in the tropical mixed deciduous forest of the "terai" and "bhavar" in Corbett Park; one group was found in oak-pine forest of the mountains near Naini Tal.

The total population sample from all types of survey, including the village, town and temple surveys previously reported, consisted of 21.4% adult males, 43.6% adult females, 25.5% infants, and 9.5% juveniles. The percentages of males, females, and infants were generally similar throughout all types of survey groups, but there were significant differences in the percentages of juveniles. Roadside and canal bank groups had less than 6% juveniles; railroad, village and town groups had approximately 10% juveniles; whereas temple and forest groups had 22% and 27% juveniles respectively. All groups except temple and forest groups are subjected to intensive trapping pressure to obtain juvenile monkeys for export.

We believe that the rhesus populations of India are declining because of: (1) changing attitudes

of Indian villagers toward monkeys, so that monkeys are no longer protected as extensively as in former years, (2) intensive trapping to obtain monkeys for export, (3) changing patterns of land use, including the deterioration of roadside habitats, and commercial forest management.

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THE INFLUENCE OF INTERSPECIFIC COMPETITION AND OTHER FACTORS ON THE DISTRIBUTION OF THE BARNACLE *CHTHAMALUS STELLATUS*

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INTRODUCTION

Most of the evidence for the occurrence of interspecific competition in animals has been gained from laboratory populations. Because of the small amount of direct evidence for its occurrence in nature, competition has sometimes been assigned a minor role in determining the composition of animal communities.

Indirect evidence exists, however, which suggests that competition may sometimes be responsible for the distribution of animals in nature. The range of distribution of a species may be decreased in the presence of another species with similar requirements (Beauchamp and Ull-yott 1932, Endean, Kenny and Stephenson 1956). Uniform distribution in space is usually attributed to intraspecific competition (Holme 1950, Clark and Evans 1954). When animals with similar requirements, such as 2 or more closely related species, are found coexisting in the same area, careful analysis usually indicates that they are not actually competing with each other (Lack 1954, MacArthur 1958).

In the course of an investigation of the animals of an intertidal rocky shore I noticed that the adults of 2 species of barnacles occupied 2 separate horizontal zones with a small area of overlap, whereas the young of the species from the upper zone were found in much of the lower zone. The upper species, *Chthamalus stellatus* (Poli) thus settled but did not survive in the

lower zone. It seemed probable that this species was eliminated by the lower one, *Balanus balanoides* (L), in a struggle for a common requisite which was in short supply. In the rocky intertidal region, space for attachment and growth is often extremely limited. This paper is an account of some observations and experiments designed to test the hypothesis that the absence in the lower zone of adults of *Chthamalus* was due to interspecific competition with *Balanus* for space. Other factors which may have influenced the distribution were also studied. The study was made at Millport, Isle of Cumbrae, Scotland.

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Distribution of the species of barnacles

The upper species, *Chthamalus stellatus*, has its center of distribution in the Mediterranean; it reaches its northern limit in the Shetland Islands, north of Scotland. At Millport, adults of this species occur between the levels of mean high water of neap and spring tides (M.H.W.N. and M.H.W.S.: see Figure 5 and Table I). In southwest England and Ireland, adult *Chtham-*

alus occur at moderate population densities throughout the intertidal zone, more abundantly when *Balanus balanoides* is sparse or absent (Southward and Crisp 1954, 1956). At Millport the larvae settle from the plankton onto the shore mainly in September and October; some additional settlement may occur until December. The settlement is most abundant between M.H.W.S. and mean tide level (M.T.L.), in patches of rock surface left bare as a result of the mortality of *Balanus*, limpets, and other sedentary organisms. Few of the *Chthamalus* that settle below M.H.W.N. survive, so that adults are found only occasionally at these levels.

Balanus balanoides is a boreal-arctic species, reaching its southern limit in northern Spain. At Millport it occupies almost the entire intertidal region, from mean low water of spring tides (M.L.W.S.) up to the region between M.H.W.N. and M.H.W.S. Above M.H.W.N. it occurs intermingled with *Chthamalus* for a short distance. *Balanus* settles on the shore in April and May, often in very dense concentrations (see Table IV).

The main purpose of this study was to determine the cause of death of those *Chthamalus* that settled below M.H.W.N. A study which was being carried on at this time had revealed that physical conditions, competition for space, and predation by the snail *Thais lapillus* L. were among the most important causes of mortality of *Balanus balanoides*. Therefore, the observations and experiments in the present study were designed to detect the effects of these factors on the survival of *Chthamalus*.

METHODS

Intertidal barnacles are very nearly ideal for the study of survival under natural conditions. Their sessile habit allows direct observation of the survival of individuals in a group whose positions have been mapped. Their small size and dense concentrations on rocks exposed at intervals make experimentation feasible. In addition, they may be handled and transplanted without injury on pieces of rock, since their opercular plates remain closed when exposed to air.

The experimental area was located on the Isle of Cumbrae in the Firth of Clyde, Scotland. Farland Point, where the study was made, comprises the southeast tip of the island; it is exposed to moderate wave action. The shore rock consists mainly of old red sandstone, arranged in a series of ridges, from 2 to 6 ft high, oriented at right angles to the shoreline. A more detailed description is given by Connell (1961). The

other barnacle species present were *Balanus crenatus* Brug and *Verruca stroemia* (O. F. Muller), both found in small numbers only at and below M.L.W.S.

To measure the survival of *Chthamalus*, the positions of all individuals in a patch were mapped. Any barnacles which were empty or missing at the next examination of this patch must have died in the interval, since emigration is impossible. The mapping was done by placing thin glass plates (lantern slide cover glasses, 10.7×8.2 cm, area 87.7 cm^2) over a patch of barnacles and marking the position of each *Chthamalus* on it with glass-marking ink. The positions of the corners of the plate were marked by drilling small holes in the rock. Observations made in subsequent censuses were noted on a paper copy of the glass map.

The study areas were chosen by searching for patches of *Chthamalus* below M.H.W.N. in a stretch of shore about 50 ft long. When 8 patches had been found, no more were looked for. The only basis for rejection of an area in this search was that it contained fewer than 50 *Chthamalus* in an area of about $1/10 \text{ m}^2$. Each numbered area consisted of one or more glass maps located in the $1/10 \text{ m}^2$. They were mapped in March and April, 1954, before the main settlement of *Balanus* began in late April.

Very few *Chthamalus* were found to have settled below mid-tide level. Therefore pieces of rock bearing *Chthamalus* were removed from levels above M.H.W.N. and transplanted to and below M.T.L. A hole was drilled through each piece; it was then fastened to the rock by a stainless steel screw driven into a plastic screw anchor fitted into a hole drilled into the rock. A hole $3/4$ " in diameter and 1" deep was found to be satisfactory. The screw could be removed and replaced repeatedly and only one stone was lost in the entire period.

For censusing, the stones were removed during a low tide period, brought to the laboratory for examination, and returned before the tide rose again. The locations and arrangements of each area are given in Table I; the transplanted stones are represented by areas 11 to 15.

The effect of competition for space on the survival of *Chthamalus* was studied in the following manner: After the settlement of *Balanus* had stopped in early June, having reached densities of $49/\text{cm}^2$ on the experimental areas (Table I) a census of the surviving *Chthamalus* was made on each area (see Figure 1). Each map was then divided so that about half of the number of

TABLE I. Description of experimental areas*

Area no.	Height in ft from M.T.L.	% of time sub- merged	POPULATION DENSITY: NO./CM ² IN JUNE, 1954			Remarks
			<i>Chthamalus</i> , autumn 1953 settlement		All barnacles, undisturbed portion	
			Undisturbed portion	Portion without <i>Balanus</i>		
MHWS.....	+4.9	4	—	—	—	—
1.....	+4.2	9	2.2	—	19.2	Vertical, partly protected
2.....	+3.5	16	5.2	4.2	—	Vertical, wave beaten
MHWN.....	+3.1	21	—	—	—	—
3a.....	+2.2	30	0.6	0.6	30.9	Horizontal, wave beaten
3b.....	"	"	0.5	0.7	29.2	" " "
4.....	+1.4	38	1.9	0.6	—	30° to vertical, partly protected
5.....	+1.4	"	2.4	1.2	—	" " " " "
6.....	+1.0	42	1.1	1.9	38.2	Horizontal, top of a boulder, partly protected
7a.....	+0.7	44	1.3	2.0	49.3	Vertical, protected
7b.....	"	"	2.3	2.0	51.7	" "
11a.....	0.0	50	1.0	0.6	32.0	Vertical, protected
11b.....	"	"	0.2	0.3	—	" "
12a.....	0.0	100	1.2	1.2	18.8	Horizontal, immersed in tide pool
12b.....	"	100	0.8	0.9	—	" " " " "
13a.....	-1.0	58	4.9	4.1	29.5	Vertical, wave beaten
13b.....	"	"	3.1	2.4	—	" " "
14a.....	-2.5	71	0.7	1.1	—	45° angle, wave beaten
14b.....	"	"	1.0	1.0	—	" " " "
MLWN.....	-3.0	77	—	—	—	—
MLWS.....	-5.1	96	—	—	—	—
15.....	+1.0	42	32.0	—	—	{ <i>Chthamalus</i> of autumn, 1954 set- tlement; densities of Oct., 1954.
7b.....	+0.7	44	5.5	3.7	—	

* The letter "a" following an area number indicates that this area was enclosed by a cage; "b" refers to a closely adjacent area which was not enclosed. All areas faced either east or south except 7a and 7b, which faced north.

Chthamalus were in each portion. One portion was chosen (by flipping a coin), and those *Balanus* which were touching or immediately surrounding each *Chthamalus* were carefully removed with a needle; the other portion was left untouched. In this way it was possible to measure the effect on the survival of *Chthamalus* both of intraspecific competition alone and of competition with *Balanus*. It was not possible to have the numbers or population densities of *Chthamalus* exactly equal on the 2 portions of each area. This was due to the fact that, since *Chthamalus* often occurred in groups, the *Balanus* had to be removed from around all the members of a group to ensure that no crowding by *Balanus* occurred. The densities of *Chthamalus* were very low, however, so that the slight differences in density

between the 2 portions of each area can probably be disregarded; intraspecific crowding was very seldom observed. Censuses of the *Chthamalus* were made at intervals of 4-6 weeks during the next year; notes were made at each census of factors such as crowding, undercutting or smothering which had taken place since the last examination. When necessary, *Balanus* which had grown until they threatened to touch the *Chthamalus* were removed in later examinations.

To study the effects of different degrees of immersion, the areas were located throughout the tidal range, either *in situ* or on transplanted stones, as shown in Table I. Area 1 had been under observation for 1½ years previously. The effects of different degrees of wave shock could not be studied adequately in such a small area



FIG. 1. Area 7b. In the first photograph the large barnacles are *Balanus*, the small ones scattered in the bare patch, *Chthamalus*. The white line on the second photograph divides the undisturbed portion (right) from the portion from which *Balanus* were removed (left). A limpet, *Patella vulgata*, occurs on the left, and predatory snails, *Thais lapillus*, are visible.

of shore but such differences as existed are listed in Table I.

The effects of the predatory snail, *Thais lapillus*, (synonymous with *Nucella* or *Purpura*, Clench 1947), were studied as follows: Cages of stainless steel wire netting, 8 meshes per inch, were attached over some of the areas. This mesh has an open area of 60% and previous work (Connell 1961) had shown that it did not inhibit growth or survival of the barnacles. The cages were about 4×6 inches, the roof was about an inch above the barnacles and the sides were fitted to the irregularities of the rock. They were held in place in the same manner as the transplanted stones. The transplanted stones were attached in pairs, one of each pair being enclosed in a cage (Table I).

These cages were effective in excluding all but the smallest *Thais*. Occasionally small *Thais*, $\frac{1}{2}$ to 1 cm in length, entered the cages through gaps at the line of juncture of netting and rock surface. In the concurrent study of *Balanus* (Con-

nell 1961), small *Thais* were estimated to have occurred inside the cages about 3% of the time.

All the areas and stones were established before the settlement of *Balanus* began in late April, 1954. Thus the *Chthamalus* which had settled naturally on the shore were then of the 1953 year class and all about 7 months old. Some *Chthamalus* which settled in the autumn of 1954 were followed until the study was ended in June, 1955. In addition some adults which, judging from their large size and the great erosion of their shells, must have settled in 1952 or earlier, were present on the transplanted stones. Thus records were made of at least 3 year-classes of *Chthamalus*.

RESULTS

The effects of physical factors

In Figures 2 and 3, the dashed line indicates the survival of *Chthamalus* growing without contact with *Balanus*. The suffix "a" indicates that the area was protected from *Thais* by a cage.

In the absence of *Balanus* and *Thais*, and protected by the cages from damage by water-borne objects, the survival of *Chthamalus* was good at all levels. For those which had settled normally on the shore (Fig. 2), the poorest survival was on the lowest area, 7a. On the transplanted stones (Fig. 3, area 12), constant immersion in a tide pool resulted in the poorest survival. The reasons for the trend toward slightly greater mortality as the degree of immersion increased are unknown. The amount of attached algae on the stones in the tide pool was much greater than on the other areas. This may have reduced the flow of water and food or have interfered directly with feeding movements. Another possible indirect effect of increased immersion is the increase in predation by the snail, *Thais lapillus*, at lower levels.

Chthamalus is tolerant of a much greater degree of immersion than it normally encounters. This is shown by the survival for a year on area 12 in a tide pool, together with the findings of Fischer (1928) and Barnes (1956a), who found that *Chthamalus* withstood submersion for 12 and 22 months, respectively. Its absence below M.T.L. can probably be ascribed either to a lack of initial settlement or to poor survival of newly settled larvae. Lewis and Powell (1960) have suggested that the survival of *Chthamalus* may be

favored by increased light or warmth during emersion in its early life on the shore. These conditions would tend to occur higher on the shore in Scotland than in southern England.

The effects of wave action on the survival of *Chthamalus* are difficult to assess. Like the degree of immersion, the effects of wave action may act indirectly. The areas 7 and 12, where relatively poor survival was found, were also the areas of least wave action. Although *Chthamalus* is usually abundant on wave beaten areas and absent from sheltered bays in Scotland, Lewis and Powell (1960) have shown that in certain sheltered bays it may be very abundant. Hatton (1938) found that in northern France, settlement and growth rates were greater in wave-beaten areas at M.T.L., but, at M.H.W.N., greater in sheltered areas.

At the upper shore margins of distribution *Chthamalus* evidently can exist higher than *Balanus* mainly as a result of its greater tolerance to heat and/or desiccation. The evidence for this was gained during the spring of 1955. Records from a tide and wave gauge operating at this time about one-half mile north of the study area showed that a period of neap tides had coincided with an unusual period of warm calm weather in April so that for several days no water, not even waves, reached the level of Area 1. In the period

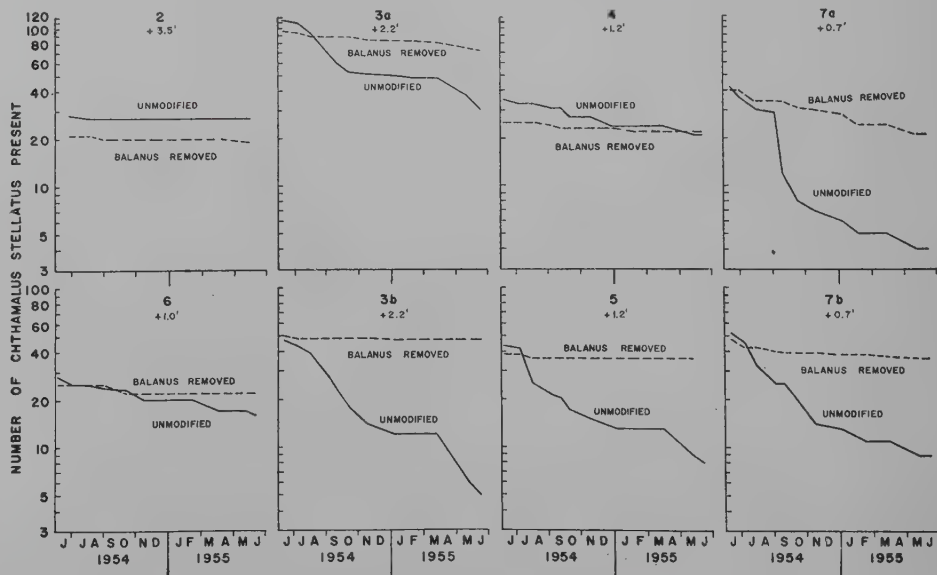


FIG. 2. Survivorship curves of *Chthamalus stellatus* which had settled naturally on the shore in the autumn of 1953. Areas designated "a" were protected from predation by cages. In each area the survival of *Chthamalus* growing without contact with *Balanus* is compared to that in the undisturbed area. For each area the vertical distance in feet from M.T.L. is shown.

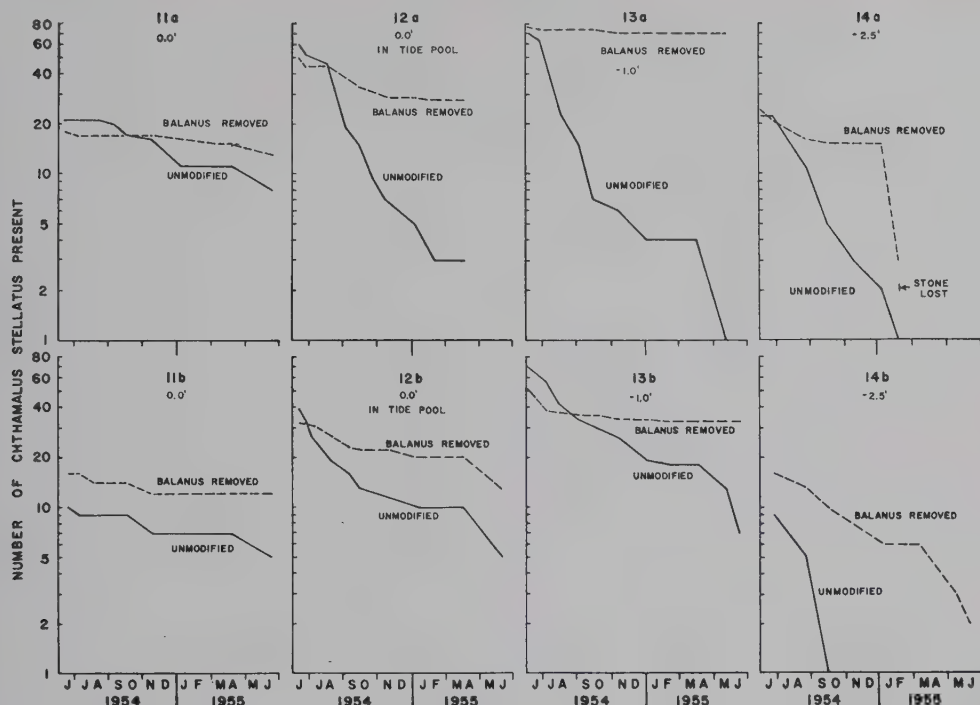


FIG. 3. Survivorship curves of *Chthamalus stellatus* on stones transplanted from high levels. These had settled in the autumn of 1953; the arrangement is the same as that of Figure 2.

between the censuses of February and May, *Balanus* aged one year suffered a mortality of 92%, those 2 years and older, 51%. Over the same period the mortality of *Chthamalus* aged 7 months was 62%, those 1½ years and older, 2%. Records of the survival of *Balanus* at several levels below this showed that only those *Balanus* in the top quarter of the intertidal region suffered high mortality during this time (Connell 1961).

Competition for space

At each census notes were made for individual barnacles of any crowding which had occurred since the last census. Thus when one barnacle started to grow up over another this fact was noted and at the next census 4-6 weeks later the progress of this process was noted. In this way a detailed description was built up of these gradually occurring events.

Intraspecific competition leading to mortality in *Chthamalus* was a rare event. For areas 2 to 7, on the portions from which *Balanus* had been removed, 167 deaths were recorded in a year. Of these, only 6 could be ascribed to crowding between individuals of *Chthamalus*. On the undisturbed portions no such crowding was

observed. This accords with Hatton's (1938) observation that he never saw crowding between individuals of *Chthamalus* as contrasted to its frequent occurrence between individuals of *Balanus*.

Interspecific competition between *Balanus* and *Chthamalus* was, on the other hand, a most important cause of death of *Chthamalus*. This is shown both by the direct observations of the process of crowding at each census and by the differences between the survival curves of *Chthamalus* with and without *Balanus*. From the periodic observations it was noted that after the first month on the undisturbed portions of areas 3 to 7 about 10% of the *Chthamalus* were being covered as *Balanus* grew over them; about 3% were being undercut and lifted by growing *Balanus*; a few had died without crowding. By the end of the 2nd month about 20% of the *Chthamalus* were either wholly or partly covered by *Balanus*; about 4% had been undercut; others were surrounded by tall *Balanus*. These processes continued at a lower rate in the autumn and almost ceased during the later winter. In the spring *Balanus* resumed growth and more crowding was observed.

In Table II, these observations are summarized for the undistributed portions of all the areas. Above M.T.L., the *Balanus* tended to overgrow the *Chthamalus*, whereas at the lower levels, undercutting was more common. This same trend was evident within each group of areas, undercutting being more prevalent on area 7 than on area 3, for example. The faster growth of *Balanus* at lower levels (Hatton 1938, Barnes and Powell 1953) may have resulted in more undercutting. When *Chthamalus* was completely covered by *Balanus* it was recorded as dead; even though death may not have occurred immediately, the buried barnacle was obviously not a functioning member of the population.

TABLE II. The causes of mortality of *Chthamalus stellatus* of the 1953 year group on the undisturbed portions of each area

Area no.	Height in ft from M.T.L.	No. at start	No. of deaths in the next year	PERCENTAGE OF DEATHS RESULTING FROM:			
				Smothering by <i>Balanus</i>	Undercutting by <i>Balanus</i>	Other crowding by <i>Balanus</i>	Unknown causes
2.....	+3.5	28	1	0	0	0	100
3a.....	+2.2	111	81	61	6	10	23
3b.....	"	47	42	57	5	2	36
4.....	+1.4	34	14	21	14	0	65
5.....	+1.4	43	35	11	11	3	75
6.....	+1.0	27	11	9	0	0	91
7a.....	+0.7	42	38	21	16	53	10
7b.....	"	51	42	24	10	10	56
11a.....	0.0	21	13	54	8	0	38
11b.....	"	10	5	40	0	0	60
12a.....	0.0	60	57	19	33	7	41
12b.....	"	39	34	9	18	3	70
13a.....	-1.0	71	70	19	24	3	54
13b.....	"	69	62	18	8	3	71
14a.....	-2.5	22	21	24	42	10	24
14b.....	"	9	9	0	0	0	100
Total, 2-7.....	—	383	264	37	9	16	38
Total, 11-14.....	—	301	271	19	21	4	56

In Table II under the term "other crowding" have been placed all instances where *Chthamalus* were crushed laterally between 2 or more *Balanus*, or where *Chthamalus* disappeared in an interval during which a dense population of *Balanus* grew rapidly. For example, in area 7a the *Balanus*, which were at the high population density of 48 per cm², had no room to expand except upward and the barnacles very quickly grew into the form of tall cylinders or cones with the diameter of the opercular opening greater than

that of the base. It was obvious that extreme crowding occurred under these circumstances, but the exact cause of the mortality of the *Chthamalus* caught in this crush was difficult to ascertain.

In comparing the survival curves of Figs. 2 and 3 within each area it is evident that *Chthamalus* kept free of *Balanus* survived better than those in the adjacent undisturbed areas on all but areas 2 and 14a. Area 2 was in the zone where adults of *Balanus* and *Chthamalus* were normally mixed; at this high level *Balanus* evidently has no influence on the survival of *Chthamalus*. On Stone 14a, the survival of *Chthamalus* without *Balanus* was much better until January when a starfish, *Asterias rubens* L., entered the cage and ate the barnacles.

Much variation occurred on the other 14 areas. When the *Chthamalus* growing without contact with *Balanus* are compared with those on the adjacent undisturbed portion of the area, the survival was very much better on 10 areas and moderately better on 4. In all areas, some *Chthamalus* in the undisturbed portions escaped severe crowding. Sometimes no *Balanus* happened to settle close to a *Chthamalus*, or sometimes those which did died soon after settlement. In some instances, *Chthamalus* which were being undercut by *Balanus* attached themselves to the *Balanus* and so survived. Some *Chthamalus* were partly covered by *Balanus* but still survived. It seems probable that in the 4 areas, nos. 4, 6, 11a, and 11b, where *Chthamalus* survived well in the presence of *Balanus*, a higher proportion of the *Chthamalus* escaped death in one of these ways.

The fate of very young *Chthamalus* which settled in the autumn of 1954 was followed in detail in 2 instances, on stone 15 and area 7b. The *Chthamalus* on stone 15 had settled in an irregular space surrounded by large *Balanus*. Most of the mortality occurred around the edges of the space as the *Balanus* undercut and lifted the small *Chthamalus* nearby. The following is a tabulation of all the deaths of young *Chthamalus* between Sept. 30, 1954 and Feb. 14, 1955, on Stone 15, with the associated situations:

Lifted by <i>Balanus</i>	: 29
Crushed by <i>Balanus</i>	: 4
Smothered by <i>Balanus</i> and <i>Chthamalus</i>	: 2
Crushed between <i>Balanus</i> and <i>Chthamalus</i>	: 1
Lifted by <i>Chthamalus</i>	: 1
Crushed between two other <i>Chthamalus</i>	: 1
Unknown	: 3

This list shows that crowding of newly settled *Chthamalus* by older *Balanus* in the autumn main-

ly takes the form of undercutting, rather than of smothering as was the case in the spring. The reason for this difference is probably that the *Chthamalus* are more firmly attached in the spring so that the fast growing young *Balanus* grow up over them when they make contact. In the autumn the reverse is the case, the *Balanus* being firmly attached, the *Chthamalus* weakly so.

Although the settlement of *Chthamalus* on Stone 15 in the autumn of 1954 was very dense, 32/cm², so that most of them were touching another, only 2 of the 41 deaths were caused by intraspecific crowding among the *Chthamalus*. This is in accord with the findings from the 1953 settlement of *Chthamalus*.

The mortality rates for the young *Chthamalus* on area 7b showed seasonal variations. Between October 10, 1954 and May 15, 1955 the relative mortality rate per day $\times 100$ was 0.14 on the undisturbed area and 0.13 where *Balanus* had been removed. Over the next month, the rate increased to 1.49 on the undisturbed area and 0.22 where *Balanus* was absent. Thus the increase in mortality of young *Chthamalus* in late spring was also associated with the presence of *Balanus*.

Some of the stones transplanted from high to low levels in the spring of 1954 bore adult *Chthamalus*. On 3 stones, records were kept of the survival of these adults, which had settled in the autumn of 1952 or in previous years and were at least 20 months old at the start of the experiment. Their mortality is shown in Table III; it was always much greater when *Balanus* was not removed. On 2 of the 3 stones this mortality rate was almost as high as that of the younger group. These results suggest that any *Chthamalus* that managed to survive the competition for space with *Balanus* during the first year would probably be eliminated in the 2nd year.

Censuses of *Balanus* were not made on the experimental areas. However, on many other areas in the same stretch of shore the survival of *Balanus* was being studied during the same period (Connell 1961). In Table IV some mortality rates measured in that study are listed; the *Balanus* were members of the 1954 settlement at population densities and shore levels similar to those of the present study. The mortality rates of *Balanus* were about the same as those of *Chthamalus* in similar situations except at the highest level, area 1, where *Balanus* suffered much greater mortality than *Chthamalus*. Much of this mortality was caused by intraspecific crowding at all levels below area 1.

TABLE III. Comparison of the mortality rates of young and older *Chthamalus stellatus* on transplanted stones

Stone No.	Shore level	Treatment	Number of <i>Chthamalus</i> present in June, 1954		% mortality over one year (or for 6 months for 14a) of <i>Chthamalus</i>	
			1953 year group	1952 or older year groups	1953 year group	1952 or older year groups
13b	1.0 ft below MTL	<i>Balanus</i> removed	51	3	35	0
		Undisturbed	69	16	90	31
12a	MTL, in a tide pool, caged	<i>Balanus</i> removed	50	41	44	37
		Undisturbed	60	31	95	71
14a	2.5 ft below MTL, caged	<i>Balanus</i> removed	25	45	40	36
		Undisturbed	22	8	86	75

TABLE IV. Comparison of annual mortality rates of *Chthamalus stellatus* and *Balanus balanoides**

Area no.	<i>Chthamalus stellatus</i> , autumn 1953 settlement		
	Height in ft from M.T.L.	Population density: no./cm ² June, 1954	% mortality in the next year
1.....	+4.2	21	17
3a.....	+2.2	31	72
3b.....	"	29	89
6.....	+1.0	38	41
7a.....	+0.7	49	90
7b.....	"	52	82
11a.....	0.0	32	62
13a.....	-1.0	29	99
12a.....	(tide pool)	19	95
1 (top).....	<i>Balanus balanoides</i> , spring 1954 settlement		
	Height in ft from M.T.L.	Population density: no./cm ² June, 1954	% mortality in the next year
1 (top).....	+4.2	21	99
1:Middle Cage 1..	+2.1	85	92
1:Middle Cage 2..	"	25	77
1:Low Cage 1....	+1.5	26	88
Stone 1.....	-0.9	26	86
Stone 2.....	"	68	94

* Population density includes both species. The mortality rates of *Chthamalus* refer to those on the undisturbed portions of each area. The data and area designations for *Balanus* were taken from Connell (1961); the present area 1 is the same as that designated 1 (top) in that paper.

In the observations made at each census it appeared that *Balanus* was growing faster than *Chthamalus*. Measurements of growth rates of the 2 species were made from photographs of

the areas taken in June and November, 1954. Barnacles growing free of contact with each other were measured; the results are given in Table V. The growth rate of *Balanus* was greater than that of *Chthamalus* in the experimental areas; this agrees with the findings of Hatton (1938) on the shore in France and of Barnes (1956a) for continual submergence on a raft at Millport.

TABLE V. Growth rates of *Chthamalus stellatus* and *Balanus balanoides*. Measurements were made of uncrowded individuals on photographs of areas 3a, 3b and 7b. Those of *Chthamalus* were made on the same individuals on both dates; of *Balanus*, representative samples were chosen

	CHTHAMALUS		BALANUS	
	No. measured	Average size, mm.	No. measured	Average size, mm.
June 11, 1954.....	25	2.49	39	1.87
November 3, 1954.....	25	4.24	27	4.83
Average size in the interval.....	3.36		3.35	
Absolute growth rate per day x 100	1.21		2.04	

After a year of crowding the average population densities of *Balanus* and *Chthamalus* remained in the same relative proportion as they had been at the start, since the mortality rates were about the same. However, because of its faster growth, *Balanus* occupied a relatively greater area and, presumably, possessed a greater biomass relative to that of *Chthamalus* after a year.

The faster growth of *Balanus* probably accounts for the manner in which *Chthamalus* were crowded by *Balanus*. It also accounts for the sinuosity of the survival curves of *Chthamalus* growing in contact with *Balanus*. The mortality rate of these *Chthamalus*, as indicated by the slope of the curves in Figs. 2 and 3, was greatest in summer, decreased in winter and increased again in spring. The survival curves of *Chthamalus* growing without contact with *Balanus* do not show these seasonal variations which, therefore, cannot be the result of the direct action of physical factors such as temperature, wave action or rain.

Seasonal variations in growth rate of *Balanus* correspond to these changes in mortality rate of *Chthamalus*. In Figure 4 the growth of *Balanus* throughout the year as studied on an intertidal panel at Millport by Barnes and Powell (1953), is compared to the survival of *Chthamalus* at about the same intertidal level in the present study. The increased mortality of *Chthamalus* was found to occur in the same seasons as the in-

creases in the growth rate of *Balanus*. The correlation was tested using the Spearman rank correlation coefficient. The absolute increase in diameter of *Balanus* in each month, read from the curve of growth, was compared to the percentage mortality of *Chthamalus* in the same month. For the 13 months in which data for *Chthamalus* was available, the correlation was highly significant, $P = .01$.

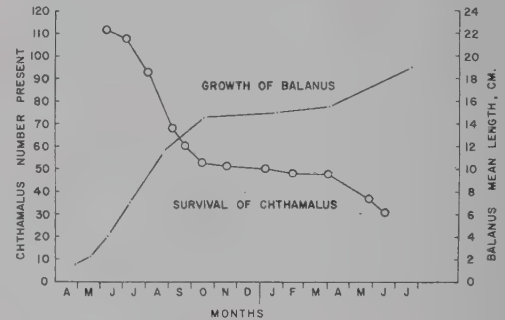


FIG. 4. A comparison of the seasonal changes in the growth of *Balanus balanoides* and in the survival of *Chthamalus stellatus* being crowded by *Balanus*. The growth of *Balanus* was that of panel 3, Barnes and Powell (1953), just above M.T.L. on Keppel Pier, Millport, during 1951-52. The *Chthamalus* were on area 3a of the present study, one-half mile south of Keppel Pier, during 1954-55.

From all these observations it appears that the poor survival of *Chthamalus* below M.H.W.N. is a result mainly of crowding by dense populations of faster growing *Balanus*.

At the end of the experiment in June, 1955, the surviving *Chthamalus* were collected from 5 of the areas. As shown in Table VI, the average size was greater in the *Chthamalus* which had grown free of contact with *Balanus*; in every case the difference was significant ($P < .01$, Mann-Whitney U. test, Siegel 1956). The survivors on the undisturbed areas were often misshapen, in some cases as a result of being lifted on to the side of an undercutting *Balanus*. Thus the smaller size of these barnacles may have been due to disturbances in the normal pattern of growth while they were being crowded.

These *Chthamalus* were examined for the presence of developing larvae in their mantle cavities. As shown in Table VI, in every area the proportion of the uncrowded *Chthamalus* with larvae was equal to or more often slightly greater than on the crowded areas. The reason for this may be related to the smaller size of the crowded *Chthamalus*. It is not due to separation, since *Chthamalus* can self-fertilize (Barnes and Crisp

TABLE VI. The effect of crowding on the size and presence of larvae in *Chthamalus stellatus*, collected in June, 1955

Area	Treatment	Level, feet above M.F.L.	Number of <i>Chthamalus</i>	DIAMETER IN MM		% of individuals which had larvae in mantle cavity
				Average	Range	
3a.....	Undisturbed	2.2	18	3.5	2.7-4.6	61
".....	<i>Balanus</i> removed	"	50	4.1	3.0-5.5	65
4.....	Undisturbed	1.4	16	2.3	1.8-3.2	81
".....	<i>Balanus</i> removed	"	37	3.7	2.5-5.1	100
5.....	Undisturbed	1.4	7	3.3	2.8-3.7	70
".....	<i>Balanus</i> removed	"	13	4.0	3.5-4.5	100
6.....	Undisturbed	1.0	13	2.8	2.1-3.9	100
".....	<i>Balanus</i> removed	"	14	4.1	3.0-5.2	130
7a & b.....	Undisturbed	0.7	10	3.5	2.7-4.5	70
".....	<i>Balanus</i> removed	"	23	4.3	3.0-6.3	81

1956). Moore (1935) and Barnes (1953) have shown that the number of larvae in an individual of *Balanus balanoides* increases with increase in volume of the parent. Comparison of the cube of the diameter, which is proportional to the volume, of *Chthamalus* with and without *Balanus* shows that the volume may be decreased to $\frac{1}{4}$ normal size when crowding occurs. Assuming that the relation between larval numbers and volume in *Chthamalus* is similar to that of *Balanus*, a decrease in both frequency of occurrence and abundance of larvae in *Chthamalus* results from competition with *Balanus*. Thus the process described in this paper satisfies both aspects of interspecific competition as defined by Elton and Miller (1954): "in which one species affects the population of another by a process of interference, i.e., by reducing the reproductive efficiency or increasing the mortality of its competitor."

The effect of predation by *Thais*

Cages which excluded *Thais* had been attached on 6 areas (indicated by the letter "a" following the number of the area). Area 14 was not included in the following analysis since many starfish were observed feeding on the barnacles at this level; one entered the cage in January, 1955, and ate most of the barnacles.

Thais were common in this locality, feeding on barnacles and mussels, and reaching average population densities of 200/m² below M.T.L. (Connell 1961). The mortality rates for *Chthamalus* in cages and on adjacent areas outside cages (indicated by the letter "b" after the number) are shown on Table VII.

If the mortality rates of *Chthamalus* growing without contact with *Balanus* are compared in and out of the cages, it can be seen that at the upper levels mortality is greater inside the cages,

TABLE VII. The effect of predation by *Thais lapillus* on the annual mortality rate of *Chthamalus stellatus* in the experimental areas*

Area	Height in ft from M.T.L.	% mortality of <i>Chthamalus</i> over a year (The initial numbers are given in parentheses)					
		a: Protected from predation by a cage			b: Unprotected, open to predation		
		With <i>Balanus</i>	Without <i>Balanus</i>	Difference	With <i>Balanus</i>	Without <i>Balanus</i>	Difference
Area 3...	+2.2	73 (112)	25 (96)	48	89 (47)	6 (50)	83
Area 7...	+0.7	90 (42)	47 (40)	43	82 (51)	23 (47)	59
Area 11...	0	62 (21)	28 (18)	34	50 (10)	25 (16)	25
Area 12...	0†	100 (60)	53 (50)	47	87 (39)	59 (32)	28
Area 13...	-1.0	98 (72)	9 (77)	89	90 (69)	35 (51)	55

*The records for 12a extend over only 10 months; for purposes of comparison the mortality rate for 12a has been multiplied by 1.2.

†Tide pool.

at lower levels greater outside. Densities of *Thais* tend to be greater at and below M.T.L. so that this trend in the mortality rates of *Chthamalus* may be ascribed to an increase in predation by *Thais* at lower levels.

Mortality of *Chthamalus* in the absence of *Balanus* was appreciably greater outside than inside the cage only on area 13. In the other 4 areas it seems evident that few *Chthamalus* were being eaten by *Thais*. In a concurrent study of the behavior of *Thais* in feeding on *Balanus balanoides*, it was found that *Thais* selected the larger individuals as prey (Connell 1961). Since *Balanus* after a few month's growth was usually larger than *Chthamalus*, it might be expected that *Thais* would feed on *Balanus* in preference to *Chthamalus*. In a later study (unpublished) made at Santa Barbara, California, *Thais emarginata* Deshayes were enclosed in cages on the shore with mixed populations of *Balanus glandula* Darwin and *Chthamalus fissus* Darwin. These species were each of the same size range as the corresponding species at Millport. It was found that *Thais emarginata* fed on *Balanus glandula* in preference to *Chthamalus fissus*.

As has been indicated, much of the mortality of *Chthamalus* growing naturally intermingled with *Balanus* was a result of direct crowding by *Balanus*. It therefore seemed reasonable to take the difference between the mortality rates of *Chthamalus* with and without *Balanus* as an index of the degree of competition between the species. This difference was calculated for each area and is included in Table VII. If these differences are compared between each pair of adjacent areas in and out of a cage, it appears that the difference, and therefore the degree of competition, was greater outside the cages at the upper shore levels and less outside the cages at the lower levels.

Thus as predation increased at lower levels, the degree of competition decreased. This result would have been expected if *Thais* had fed upon *Balanus* in preference to *Chthamalus*. The general effect of predation by *Thais* seems to have been to lessen the interspecific competition below M.T.L.

DISCUSSION

"Although animal communities appear qualitatively to be constructed as if competition were regulating their structure, even in the best studied cases there are nearly always difficulties and unexplored possibilities" (Hutchinson 1957).

In the present study direct observations at intervals showed that competition was occurring under natural conditions. In addition, the evidence is strong that the observed competition with *Balanus* was the principal factor determining the local distribution of *Chthamalus*. *Chthamalus* thrived at lower levels when it was not growing in contact with *Balanus*.

However, there remain unexplored possibilities. The elimination of *Chthamalus* requires a dense population of *Balanus*, yet the settlement of *Balanus* varied from year to year. At Millport, the settlement density of *Balanus balanoides* was measured for 9 years between 1944 and 1958 (Barnes 1956b, Connell 1961). Settlement was light in 2 years, 1946 and 1958. In the 3 seasons of *Balanus* settlement studied in detail, 1953-55, there was a vast oversupply of larvae ready for settlement. It thus seems probable that most of the *Chthamalus* which survived in a year of poor settlement of *Balanus* would be killed in competition with a normal settlement the following year. A succession of years with poor settlements of *Balanus* is a possible, but improbable occurrence at Millport, judging from the past record. A very light settlement is probably the result of a chance combination of unfavorable weather circumstances during the planktonic period (Barnes 1956b). Also, after a light settlement, survival on the shore is improved, owing principally to the reduction in intraspecific crowding (Connell 1961); this would tend to favor a normal settlement the following year, since barnacles are stimulated to settle by the presence of members of their own species already attached on the surface (Knight-Jones 1953).

The fate of those *Chthamalus* which had survived a year on the undisturbed areas is not known since the experiment ended at that time. It is probable, however, that most of them would have been eliminated within 6 months; the mortality rate had increased in the spring (Figs. 2

and 3), and these survivors were often misshapen and smaller than those which had not been crowded (Table VI). Adults on the transplanted stones had suffered high mortality in the previous year (Table III).

Another difficulty was that *Chthamalus* was rarely found to have settled below mid tide level at Millport. The reasons for this are unknown; it survived well if transplanted below this level, in the absence of *Balanus*. In other areas of the British Isles (in southwest England and Ireland, for example) it occurs below mid tide level.

The possibility that *Chthamalus* might affect *Balanus* deleteriously remains to be considered. It is unlikely that *Chthamalus* could cause much mortality of *Balanus* by direct crowding; its growth is much slower, and crowding between individuals of *Chthamalus* seldom resulted in death. A dense population of *Chthamalus* might deprive larvae of *Balanus* of space for settlement. Also, *Chthamalus* might feed on the planktonic larvae of *Balanus*; however, this would occur in March and April when both the sea water temperature and rate of cirral activity (presumably correlated with feeding activity), would be near their minima (Southward 1955).

The indication from the caging experiments that predation decreased interspecific competition suggests that the action of such additional factors tends to reduce the intensity of such interactions in natural conditions. An additional suggestion in this regard may be made concerning parasitism. Crisp (1960) found that the growth rate of *Balanus balanoides* was decreased if individuals were infected with the isopod parasite *Hemioniscus balani* (Spence Bate). In Britain this parasite has not been reported from *Chthamalus stellatus*. Thus if this parasite were present, both the growth rate of *Balanus*, and its ability to eliminate *Chthamalus*, would be decreased, with a corresponding lessening of the degree of competition between the species.

The causes of zonation

The evidence presented in this paper indicates that the lower limit of the intertidal zone of *Chthamalus stellatus* at Millport was determined by interspecific competition for space with *Balanus balanoides*. *Balanus*, by virtue of its greater population density and faster growth, eliminated most of the *Chthamalus* by directing crowding.

At the upper limits of the zones of these species no interaction was observed. *Chthamalus* evidently can exist higher on the shore than *Balanus* mainly as a result of its greater tolerance to heat and/or desiccation.

The upper limits of most intertidal animals are probably determined by physical factors such as these. Since growth rates usually decrease with increasing height on the shore, it would be less likely that a sessile species occupying a higher zone could, by competition for space, prevent a lower one from extending upwards. Likewise, there has been, as far as the author is aware, no study made which shows that predation by land species determines the upper limit of an intertidal animal. In one of the most thorough of such studies, Drinnan (1957) indicated that intense predation by birds accounted for an annual mortality of 22% of cockles (*Cardium edule* L.) in sand flats where their total mortality was 74% per year.

In regard to the lower limits of an animal's zone, it is evident that physical factors may act directly to determine this boundary. For example, some active amphipods from the upper levels of sandy beaches die if kept submerged. However, evidence is accumulating that the lower limits of distribution of intertidal animals are determined mainly by biotic factors.

Connell (1961) found that the shorter length of life of *Balanus balanoides* at low shore levels could be accounted for by selective predation by *Thais lapillus* and increased intraspecific competition for space. The results of the experiments in the present study confirm the suggestions of other authors that lower limits may be due to interspecific competition for space. Knox (1954) suggested that competition determined the distribution of 2 species of barnacles in New Zealand. Endean, Kenny and Stephenson (1956) gave indirect evidence that competition with a colonial polychaete worm, (*Galeolaria*) may have determined the lower limit of a barnacle (*Tetraclista*) in Queensland, Australia. In turn the lower limit of *Galeolaria* appeared to be determined by competition with a tunicate, *Pyura*, or with dense algal mats.

With regard to the 2 species of barnacles in the present paper, some interesting observations have been made concerning changes in their abundance in Britain. Moore (1936) found that in southwest England in 1934, *Chthamalus stellatus* was most dense at M.H.W.N., decreasing in numbers toward M.T.L. while *Balanus balanoides* increased in numbers below M.H.W.N. At the same localities in 1951, Southward and Crisp (1954) found that *Balanus* had almost disappeared and that *Chthamalus* had increased both above and below M.H.W.N. *Chthamalus* had not reached the former densities of *Balanus* except

at one locality, Brixham. After 1951, *Balanus* began to return in numbers, although by 1954 it had not reached the densities of 1934; *Chthamalus* had declined, but again not to its former densities (Southward and Crisp 1956).

Since *Chthamalus* increased in abundance at the lower levels vacated by *Balanus*, it may previously have been excluded by competition with *Balanus*. The growth rate of *Balanus* is greater than *Chthamalus* both north and south (Hatton 1938) of this location, so that *Balanus* would be likely to win in competition with *Chthamalus*. However, changes in other environmental factors such as temperature may have influenced the abundance of these species in a reciprocal manner. In its return to southwest England after 1951, the maximum density of settlement of *Balanus* was 12 per cm²; competition of the degree observed at Millport would not be expected to occur at this density. At a higher population density, *Balanus* in southern England would probably eliminate *Chthamalus* at low shore levels in the same manner as it did at Millport.

In Loch Sween, on the Argyll Peninsula, Scotland, Lewis and Powell (1960) have described an unusual pattern of zonation of *Chthamalus stellatus*. On the outer coast of the Argyll Peninsula *Chthamalus* has a distribution similar to that at Millport. In the more sheltered waters of Loch Sween, however, *Chthamalus* occurs from above M.H.W.S. to about M.T.L., judging the distribution by its relationship to other organisms. *Balanus balanoides* is scarce above M.T.L. in Loch Sween, so that there appears to be no possibility of competition with *Chthamalus*, such as that occurring at Millport, between the levels of M.T.L. and M.H.W.N.

In Figure 5 an attempt has been made to summarize the distribution of adults and newly settled larvae in relation to the main factors which appear to determine this distribution. For *Balanus* the estimates were based on the findings of a previous study (Connell 1961); intraspecific competition was severe at the lower levels during the first year, after which predation increased in importance. With *Chthamalus*, it appears that avoidance of settlement or early mortality of those larvae which settled at levels below M.T.L., and elimination by competition with *Balanus* of those which settled between M.T.L. and M.H.W.N., were the principal causes for the absence of adults below M.H.W.N. at Millport. This distribution appears to be typical for much of western Scotland.

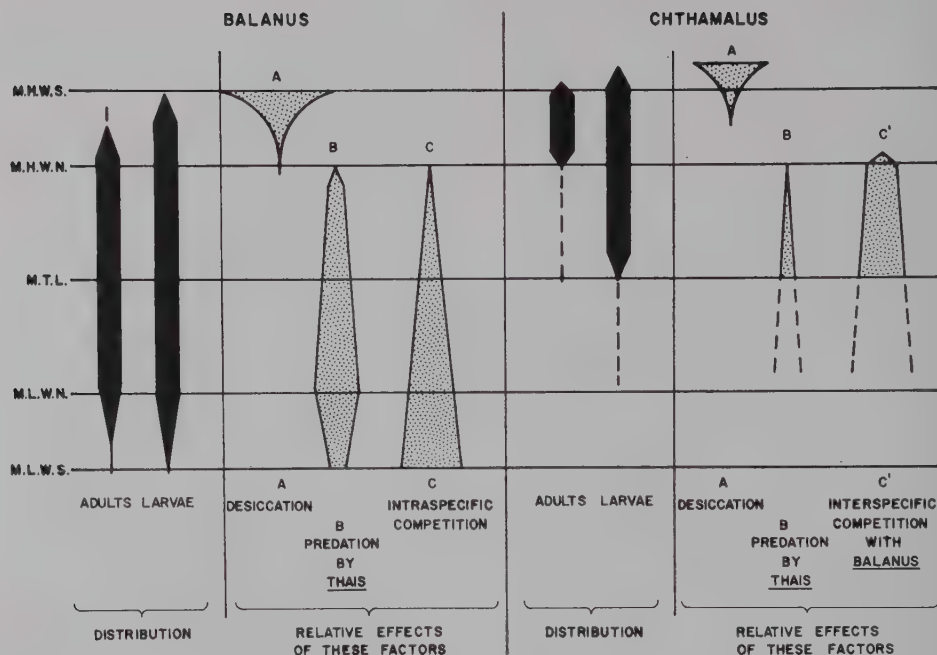


FIG. 5. The intertidal distribution of adults and newly settled larvae of *Balanus balanoides* and *Chthamalus stellatus* at Millport, with a diagrammatic representation of the relative effects of the principal limiting factors.

SUMMARY

Adults of *Chthamalus stellatus* occur in the marine intertidal in a zone above that of another barnacle, *Balanus balanoides*. Young *Chthamalus* settle in the *Balanus* zone but evidently seldom survive, since few adults are found there.

The survival of *Chthamalus* which had settled at various levels in the *Balanus* zone was followed for a year by successive censuses of mapped individuals. Some *Chthamalus* were kept free of contact with *Balanus*. These survived very well at all intertidal levels, indicating that increased time of submergence was not the factor responsible for elimination of *Chthamalus* at low shore levels. Comparison of the survival of unprotected populations with others, protected by enclosure in cages from predation by the snail, *Thais lapillus*, showed that *Thais* was not greatly affecting the survival of *Chthamalus*.

Comparison of the survival of undisturbed populations of *Chthamalus* with those kept free of contact with *Balanus* indicated that *Balanus* could cause great mortality of *Chthamalus*. *Balanus* settled in greater population densities and grew faster than *Chthamalus*. Direct observations at each census showed that *Balanus* smothered,

undercut, or crushed the *Chthamalus*; the greatest mortality of *Chthamalus* occurred during the seasons of most rapid growth of *Balanus*. Even older *Chthamalus* transplanted to low levels were killed by *Balanus* in this way. Predation by *Thais* tended to decrease the severity of this interspecific competition.

Survivors of *Chthamalus* after a year of crowding by *Balanus* were smaller than uncrowded ones. Since smaller barnacles produce fewer offspring, competition tended to reduce reproductive efficiency in addition to increasing mortality.

Mortality as a result of intraspecific competition for space between individuals of *Chthamalus* was only rarely observed.

The evidence of this and other studies indicates that the lower limit of distribution of intertidal organisms is mainly determined by the action of biotic factors such as competition for space or predation. The upper limit is probably more often set by physical factors.

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METABOLIC CHARACTERISTICS OF MOUNTAIN, DESERT AND COASTAL POPULATIONS OF *PEROMYSCUS*

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INTRODUCTION

Because of its rich taxonomic diversity the deer mouse, *Peromyscus*, has been used for many studies of speciation and natural selection. These have focused mainly on the evolutionary implications of variations in morphology, pelage color, behavior and reproductive biology. Progress along these lines has been reviewed by Blair (1950). The experiments reported here are a contribution to the investigation of physiological aspects of evolution within this genus. Measurements of meta-

bolic rate, body temperature and pelage insulation were made in order to evaluate the selective roles that might be played by the environmental variables: oxygen tension, temperature and aridity. Many of the data were organized in accordance with the model of Scholander *et al.* (1950) which formulates the expected relationships between ambient temperature, body temperature, metabolism and insulation. These relationships, in non-laboratory mammals, have also been studied by Griffin *et al.* (1953), Hart and Heroux (1953),

Dawson (1955), Irving *et al.* (1955), Pearson (1960) and others and summarized by Hart (1957).

The comparatively low oxygen tension of high mountain habitats, and the combination of aridity and high temperature in desert habitats are environmental extremes that might be important in the evolutionary history of some species, subspecies or local populations. The possible effect of differing oxygen tensions was tested by comparisons of metabolic patterns among 4 subspecies of *P. maniculatus* that were trapped in 3 high mountain localities and 4 coastal localities. Cook and Hannon (1954) measured the oxygen consumption of a sample of *P. maniculatus sonoriensis* from approximately 12,500 ft. on White Mountain, and 2 groups of *P. m. gambeli* from low elevations. They found that the high altitude mice metabolized at an average rate strikingly lower than the others. It was not possible to decide, however, whether altitude, temperature or some other factor had been the selective force responsible. Adaptations to conditions of aridity and high temperature were found by contrasting a group of *P. eremicus* trapped in desert habitats with a group of *P. maniculatus* from mountain habitats. These species are taxonomically relatively far apart; *maniculatus* is a ubiquitous form placed in the subgenus *Peromyscus*, while *eremicus*, a strictly desert inhabitant, is placed in the subgenus *Haplomyloms*.

The 3 variables measured in these experiments, metabolic rate, insulation and body temperature, are naturally interrelated in the overall pattern of thermal regulation. It became evident that a 4th factor, behavior, was important, not only as a troublesome source of experimental variation, but as an integral part of the total response of the animal to environmental factors such as high temperature. Some differences in behavior, including degrees of "nervousness," were observed and also inferred from the metabolism data. Thus the results are of interest in providing some indications of the character and magnitude of both physiological and behavioral gaps separating subspecies as contrasted with subgenera, in *Peromyscus*. An attempt is made to link the group characteristics to the ecological conditions of each habitat.

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DESCRIPTION OF HABITATS AND EXPERIMENTAL ANIMALS

The mice used in this study were maintained in an unheated garage in Berkeley, California, or in a similar unheated room on the Berkeley campus of the University of California. The room temperatures were a few degrees warmer in winter and cooler in summer than the outside air. Outside temperatures, from Oakland Airport data, have a yearly average of about 15°C. The minimum garage temperature recorded was 9.8; the maximum was 23.8.

The wild caught animals were formed into 6 experimental groups. In addition, litters were raised from pairs taken in mountain and lowland areas. These, when fully adult, formed 2 F₁ groups. Mice from Mount Rose and White Mountain were combined for one experiment. Information on capture and the taxonomic and experimental designations of each group is presented in Table I. The designations "North Coast" and "South Coast" are used for convenience in referring to the 2 coastal subspecies and do not imply any meaning in terms of latitude. The South Coast animals were taken from 3 localities which differ somewhat in floral details, but are all essentially chaparral in character, are practically identical in altitude and are subject to the mild California climate. The North Coast animals represent a subspecies that is confined to a coastal strip extending from Marin Co., California to the Columbia river. This area has a heavy winter rainfall and the chaparral habitat is often invaded or replaced by forest.

The 3 mountain habitats (see Table I) have several months of winter snowfall with low night and winter temperatures. The permanent *Peromyscus* population on White Mountain ranges over a plateau at elevations from about 10,000

TABLE I. Origins and designations of experimental animals

Designation and name	Number of mice	Locality
South Coast <i>P. m. gambeli</i>	9	Strawberry Canyon, Berkeley, Alameda Co., California
	2	near Panoche, San Benito Co., California
	4	near Jamesburg, Monterey Co., California
North Coast <i>P. m. rubidus</i>	10	near Inverness, Marin Co., California
Mount Rose Probably intergrades of <i>P. m. gambeli</i> and <i>P. m. sonoriensis</i>	9	south slope Mount Rose, 9,000-9,500 feet, Washoe Co., Nevada
White Mountain <i>P. m. sonoriensis</i>	15	White Mountain, 10,000-12,500 feet, Mono Co., California
Tetons <i>P. m. artemisiae</i>	12	east slope Teton Mountains, 9,000-10,000 feet, Teton National Park, Wyoming
<i>eremicus</i> <i>P. eremicus eremicus</i>	1	Furnace Creek Ranch, Death Valley National Monument, Inyo Co., California
	9	Borrego State Park, San Diego Co., California
	2	Walker Pass, Kern Co., California
Berkeley F ₁ <i>P. m. gambeli</i>	8	Raised in lab from two males and two females from Berkeley
White Mountain F ₁ <i>P. m. sonoriensis</i>	9	Raised in lab from two males and two females from White Mountain

to 14,000 ft, and is partly isolated from lower levels by steep, barren slopes and canyon walls. For these reasons the White Mountain group probably represented a fairly discrete high altitude population. In contrast, the Teton and Mount Rose sites were near the upper limit of continuous distribution that extends downward to about 6,000 ft. The traplines at these 2 sites probably sampled no large populations existing above 10,000 ft and, in both cases, the high altitude animals were separated only by distance from lower populations.

OXYGEN CONSUMPTION

Materials and methods

The animals were kept in captivity for 6 weeks or more before rate of oxygen consumption was measured. This was considered to be a sufficient period for acclimation to coastal conditions. Tests were made from October to March. The apparatus was a closed chamber style of respirometer similar to that described by Morrison (1947) but with the spirometer descent measured by a lever sweeping across a meter stick, in place of the automatic features of Morrison's apparatus.

Two mice were run simultaneously, each in its separate chamber-spirometer set-up. Wide-mouth quart jars placed on their sides served as chambers. The mouse was placed in a quonset-shaped wire cage that matched the contours of the jar. This cage was 12.5 cm long, 6.5 cm wide and 5.0 cm high at the midline. Calcium chloride was used to absorb water vapor. Carbon dioxide was removed by soda lime spread on the floor of the chamber as well as on one side in a fine-mesh oblong wire basket. Spot checks of carbon dioxide content of the chamber air were made with a Scholander type of syringe analyser. The average CO₂ content was 0.6%. Two analyses showed a CO₂ percentage of 1.1; all others were 1.0% or less.

The maximum variation of the water bath temperature for any one run was 0.5°C; the usual variation was 0.2°C. The temperature of the chambers, indicated by thermometers placed near the inside wall, varied as much as one degree, depending on the heat production of the mouse, but in most of the runs the chamber temperature fluctuated to the same degree as the bath, and at a slightly higher level. The values read from the inside thermometers were taken to represent ambient temperatures.

No attempt was made to insure a post-absorptive state other than to make all runs in the daytime in the period from 9:00 A M to 5:00 P M. The procedure was to allow one hour for mouse and chamber to reach equilibrium before beginning the measuring period. Readings were taken at various time intervals, as described below. All values are expressed as cc of dry gas at standard conditions.

In these determinations there were 3 biological sources of variation that were controlled as far as possible. These are discussed in order of increasing importance.

(1) *Sex*. The female's body temperature and metabolic rate are expected, statistically, to be slightly higher than those of the male (Cook and Hannon 1954, Morrison and Ryser 1959). In the present experiments the sexes separated in accordance with this expectation only in the White Mountain group. In the other determinations sex differences were not consistent. The males and females of the *eremicus* group were the closest together in average values. Both sexes were used when available in order to enlarge the experimental groups and the sex ratios were made as equal as possible.

(2) *Size*. Body weight was used as an index of size. In addition to the effect of size *per se* on

metabolism, 2 associated factors were noted. First, the large *maniculatus* gave the impression of being, as a group, more restless in the metabolism chamber than the smaller mice, even though individual large mice were often passive. If, on the average, larger mice had a different reaction to the experimental conditions, leading to an elevation of metabolic rate, the usual effect of size on metabolism would be counteracted. Second, the larger mice were always fairly fat, while smaller mice were sometimes fat and sometimes lean. The possible effect of a disproportionate distribution of any tissue such as fat in the sample would be a distortion of the usual relationship between size and metabolism. Although no such distortion was found in fat and lean porcupines (Irving *et al.* 1955), obese mice were not used.

A few males from Mount Rose happened to fall into 2 distinct weight groups. Their metabolic rates at several temperatures are plotted in Figure 1. The difference of the 2 groups at thermal neutrality is 5%, but they diverge more widely on both sides of this zone. The plot shows that, whatever contradictory components enter into the size factor, it can be a variable of important magnitude. A contrary indication, at least at low temperatures, is the interesting result of oxygen consumption measurements of *P. m. gracilis* (Hart 1953a). These mice, with a weight range of 15-26 g, tested at 1-2°C, showed no effect of weight on metabolic rate.

Experimental groups were made up, as far as possible, with a minimal range of body weights.

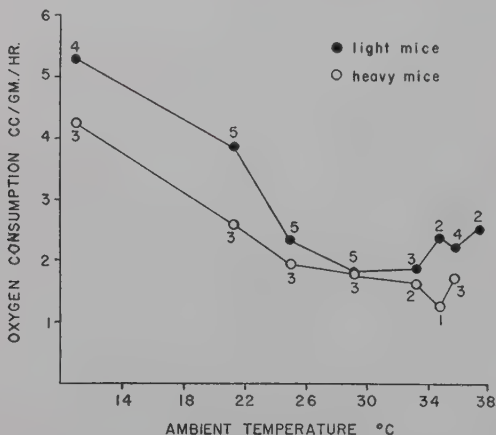


FIG. 1. Comparison of rates of oxygen consumption of 2 weight groups of males of *P. maniculatus* from Mount Rose. The heavy group consists of 3 mice with an average body weight of 27.3 grams. The mean weight of the 5 mice of the light group is 16.9 grams. Numerals next to each point indicate the number of runs.

in some cases a shortage of animals made an ideal weight distribution impossible.

(3) *Activity*. Unless otherwise specified all oxygen consumption values were derived from runs in which the effect of activity was minimized by taking readings frequently and eliminating periods of activity from the final average. Slight, discontinuous movements, if present, were not excluded by this method. Such movements consisted of short periods of fur grooming, slight head movements, or one or two turns in the cage. All other activities and any activity of a continuous nature were excluded. Short buffer periods were allowed between excluded and included periods to insure a steady state of CO₂ absorption. In most cases, by careful watching, periods of 20 to 30 minutes of continuous quiet could be located so that the data did not have to be elaborately dissected into quiet and active segments. Twenty to 40 minutes were secured for each mouse, with as many duplicate runs as possible. The resulting values can be called resting rates of metabolism and include any or all conditions from sleep to a "quiet-alert" state. Five runs are chosen from the data to illustrate the range of metabolic activity that is possible even when overt activity is at an extreme minimum (Table II). These examples show the contrast between the first part of each run in which some grooming or head movement is present, and the 2nd part, in which the mouse is completely quiet. In one of the examples no overt activity is present in either part. The average difference between the first and 2nd segments of these runs is 14.9%. Chevillard (1935) reports an even greater difference, 28.9%, between "relative repose" and "absolute repose" in the white mouse, *Mus musculus*.

One individual, a male *P. m. gambeli*, metabolized at the very low average rate of 1.01 cc/gram hour for a 30 minute period. This is similar to some low values for *P. m. gracilis* recorded by Morrison (1948). Pearson (1947) reported an even lower minimum rate for *Mus musculus*.

Metabolic rates of all groups at one ambient temperature. Experiment 1.

The results of all oxygen consumption runs at 25°C with the effect of activity eliminated, are listed in Table III.

These resting rates are plotted in Figure 2, with comparable data from the results of Cook and Hannon (1954). Fig. 2 also shows the predicted position and slope of the increase of metabolic rate in response to declining ambient temperature, as well as the estimated limits of

TABLE II. Changes in metabolic rate in quiet mice (*P. maniculatus*)

Temperature of chamber (°C)	Remarks	Length of measured period (minutes)	Oxygen consumption (cc/gm hr)	Percent difference
17.0	Quiet, one period of cleaning, some head movements; body formed into ball	20	5.33	21.7
	Completely quiet	15	4.17	
20.3	Awake, but quiet	20	4.65	14.4
	Asleep	15	3.98	
24.9	Quiet, with some head movements and two short periods of cleaning	25	3.69	17.6
	Completely quiet	10	3.04	
29.1	Quiet, one period of cleaning lasting less than one minute	10	2.41	11.6
	Quiet, body in a ball, eyes may have been closed	15	2.13	
29.1	Quiet, two slight cleaning periods	10	2.52	9.5
	Body in a ball, asleep at end of run	15	2.28	
Average difference:				14.9%

variation of this predicted slope. The metabolic data are thus compared to theoretical expectation.

The predicted positions were established as follows. The basal metabolic rate expected for mammals of the average size of those used in these experiments was calculated, using the empirical relation between metabolic rate and "metabolic surface" (Brody 1945). The result agreed quite well with the minimum values of Experiment 2 and with "basal" values for *P. m. gracilis* reported by Pearson (1947) and Morrison (1948). This basal value was plotted as a single line in the zone of thermal neutrality and was extended to intersect the limits of the lower critical temperatures, as found in Experiments 2 and 3. These intersections mark the region where a plot of metabolic rate on ambient temperature will break, *i.e.*, the basal or resting metabolism is augmented here by the metabolism of active body temperature control. Lines from this region to the resting body temperature on the abscissa determine the expected slope of the increase of metabolic rate below the zone of thermal neutrality. A theoretical discussion of these relationships is given by Scholander *et al.* (1950). The mean daytime, resting body temperature, from the results of Experiment 4, is 36.8°C. This value was marked on the abscissa. Three metab-

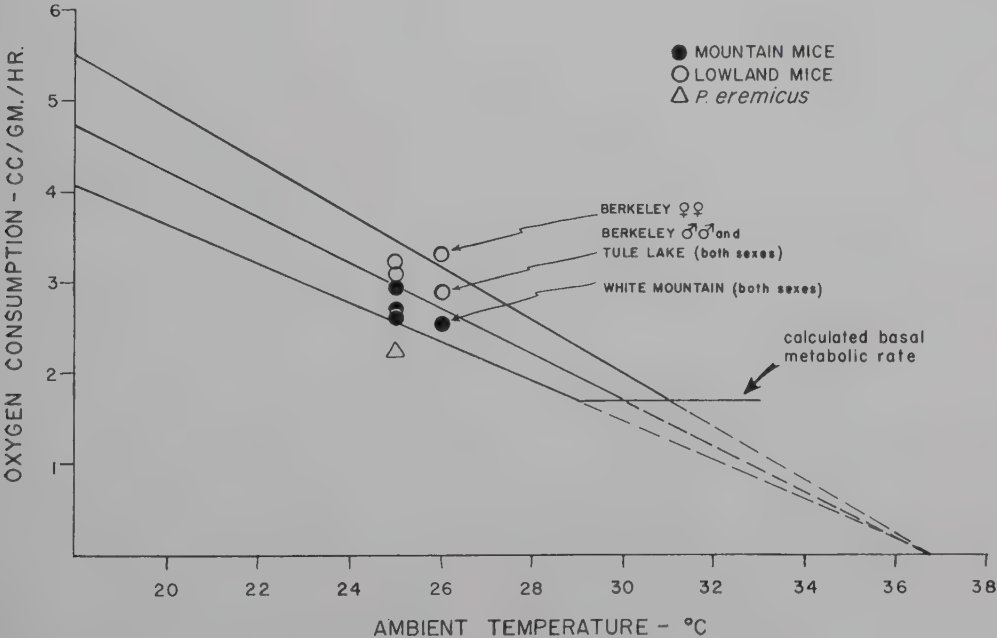


FIG. 2. Mean rates of oxygen consumption of mice tested at 25°C, plotted with the data of Cook and Hannon (1954) for mice tested at 26°C. These values are shown in relation to predicted slopes of increase of metabolic rate with decreasing ambient temperature. The 25° points are identified in Table III.

TABLE III. Oxygen consumption of 6 groups of *Peromyscus* measured at an ambient temperature of 25°C. Resting rates (activity excluded)

Group designation	Number of animals	Weight (g) average and range	Median weight	Sex ratio	cc oxygen per gm/hr	n	Standard deviation
Tetons.....	12	20.9 (17.2—29.7)	19.7	7 ♂♂ 5 ♀♀	2.62 ± .13	22	.6170
Mount Rose.....	8	21.7 (16.1—29.7)	19.6	8 ♂♂ no ♀♀	2.72 ± .15	9	.4732
North Coast.....	10	19.5 (17.0—25.9)	18.7	10 ♂♂ no ♀♀	3.11 ± .22	10	.7142
White Mountain F ₁	9	22.6 (18.2—25.7)	23.4	6 ♂♂ 3 ♀♀	2.97 ± .12	16	.4882
Berkeley F ₁	8	17.9 (15.3—21.7)	18.0	4 ♂♂ 4 ♀♀	3.26 ± .09	14	.1231
<i>eremicus</i>	4	24.7 (20.9—33.2)	21.6	2 ♂♂ 2 ♀♀	2.25 ± .04	4	.0831

olic slopes were laid out and extended to pass through the plotted data. The slope line passing through the mid-value of the range of lower critical temperatures is taken to be the best prediction, and the flanking lines passing through the upper and lower extremes of the critical temperature range are the estimated limits of variation.

Relating the experimental means to those predicted, the *eremicus* is definitely below the lowest estimated position. The *eremicus* differs significantly from both F₁ groups and the North Coast group, but not from any of the others. Its low metabolic rate, discussed in Experiment 3, cannot be related to its larger size alone. Seven of the 8 group values of *maniculatus* are encompassed by the predicted slopes. With the exception of the Berkeley F₁ group and the Berkeley females, the relative positions of the plotted values cannot be explained by differences in body size.

From Fig. 2 it appears that the metabolic rates of at least 7 of the *maniculatus* groups, recorded at 25 and 26°C, are essentially normal in relation to predictions made on the basis of the "typical" mammal. The mountain mice do not appear to be atypical, even though their means are separate from and below those of the lowland mice. Because of the difficulty of establishing precise values for the lower critical temperature and the body temperature, this conclusion is tentative. It can be said, however, that there is no positive evidence of adaptation to high altitude that involves a different intrinsic rate of metabolism. This negative indication is reinforced by the fact that, although the Teton and Mount Rose mice

were not expected to represent animals adapted to a significantly hypoxic environment, their position on the curve (Fig. 2) is very close to that of the White Mountain mice. This question is considered again in the discussion of Experiment 2.

Although none of the differences between *maniculatus* groups tested at 25° in this experiment is statistically significant, there are several reasons for thinking that biological as well as random factors played a role in the separation of the mean values. The data form a consistent pattern in which the higher values are of coastal mice, the lower values are of mountain mice. Furthermore, the mountain-lowland contrasts found by Cook and Hannon (1954), also plotted in Fig. 2, are highly significant statistically. Finally, in Experiment 2 some of the metabolic rates of one coastal group are found to differ significantly from those of the White Mountain group. There are 2 likely interpretations of these results, as follows:

(1) The variation of the lower critical temperature, as plotted in Fig. 2, implies variation in insulation. On this assumption, the Tule Lake mice, from an inland, cold winter area, might be expected to group themselves with the mountain mice. But the Tule Lake value is definitely in a "lowland" position. Similarly, the White Mountain F₁ group is in an anomalous, more or less intermediate, position. These apparent contradictions could be explained by assuming that the pelage is the major source of insulative variation. The Tule Lake mice might have been in summer pelage at the time of the tests, and the White

TABLE IV. Oxygen consumption of 4 groups of *Peromyscus* measured at an ambient temperature of 25°C. Activity included

Group designation	Number of animals	Weight (g) average and range	Median weight	Sex ratio	cc oxygen per gm/hr	n	Standard deviation
White Mountain.....	15	21.2 (17.0—25.8)	20.0	9 ♂♂ 6 ♀♀	3.47 ± .11	39	.7333
Mount Rose.....	7	19.7 (14.3—25.1)	20.0	4 ♂♂ 3 ♀♀	3.56 ± .13	27	.6951
North Coast.....	8	19.2 (14.0—23.8)	20.2	5 ♂♂ 3 ♀♀	4.49 ± .22	13	.8249
South Coast.....	13	22.0 (17.7—27.8)	21.8	9 ♂♂ 4 ♀♀	4.02 ± .07	25	.3758

Mountain lab-reared litters might have developed a light fur coat because they matured in a coastal environment. Seasonal shifts in fur density have been shown in *P. leucopus*, *P. m. bairdi* (Sealand 1951) and *P. m. rubidus* (Huestis 1931). However, analysis of the comparative values of insulation obtained in Experiment 5 show that at least some of the differences in Fig. 2 cannot be attributed to group differences in insulation. (2) The important influence on metabolism of even slight motor actions has already been shown (Table 2). Tests in which the effects of activity were not eliminated show that such effects vary significantly between some groups. In these tests, summarized in Table IV, the consumption of oxygen during only the first 30 minutes following the one hour adjustment period was measured without elimination of any part of the measured time. Thus the results include the metabolism of overt activity. This activity was extensive in some of the runs. North Coast mice, *P. m. rubidus*, appeared to be especially prone to climb about the sides of the chamber cage and gnaw at the screen. If we consider the metabolic rates in these runs as indicators of overall nervous response to the conditions of the experiment, the results show the North Coast group to be hyperactive. The 2 coastal groups do not differ significantly from each other, but the differences between both of these and both of the mountain groups are significant ($P = .01$).

The intermediate position of the White Mountain F_1 group is a result of its "normality," i.e., its rate of oxygen consumption was predicted more precisely than any other. The results of Experiment 5 show that the higher mean metabolic rate of this group, in relation to at least one of the wild caught mountain groups, is not due to inferior insulation. It is possible that laboratory conditions may have had some in-

fluence on the nervous temperament of these lab-reared mice or they may have been younger than were the wild caught individuals at the time of measurement, leading to a metabolic consequence of age differences.

The relation of metabolic rate to ambient temperature in high and low altitude mice.
Experiment 2.

In order to eliminate the thermogenic effect of ambient temperature, oxygen consumption of White Mountain and South Coast groups was measured at temperatures in the zone of thermal neutrality. To define this zone tests were made at seven different temperatures ranging from 28.5 to 36.4°C. The results are presented in Table V

TABLE V. Oxygen consumption of White Mountain and South Coast groups: summary of data plotted in Figure 3a

Temperature (°C)	WHITE MOUNTAIN			SOUTH COAST		
	cc oxygen per gm/hr	n	Standard deviation	cc oxygen per gm/hr	n	Standard deviation
28.5.....	2.75 ± .12	10	.4027	3.24 ± .12	14	.4801
29.9.....	2.45 ± .07	13	.2540	2.72 ± .16	19	.5823
30.7.....	2.31 ± .07	13	.3375	2.81 ± .12	13	.4621
31.8.....	2.27 ± .06	24	.3418	2.57 ± .07	23	.3468
33.9.....	2.28 ± .15	12	.5432	2.55 ± .08	13	.3129
35.7.....	2.60 ± .09	25	.4556	2.64 ± .07	27	.4075
36.4.....	2.89 ± .14	11	.4656	2.95 ± .09	10	.3024

and Figures 3 and 4. All values, whether means or minima, are of resting metabolic rates. The numbers of mice used in this experiment were: 13 *P. m. gambeli* and 12 *P. m. sonoriensis*.

Each group is analyzed according to sex (Fig. 3b) and size (Fig. 3c). The size comparisons were made by arbitrarily separating mice that weighed more than 22 grams from those weighing less than 22 grams. The total range of weights

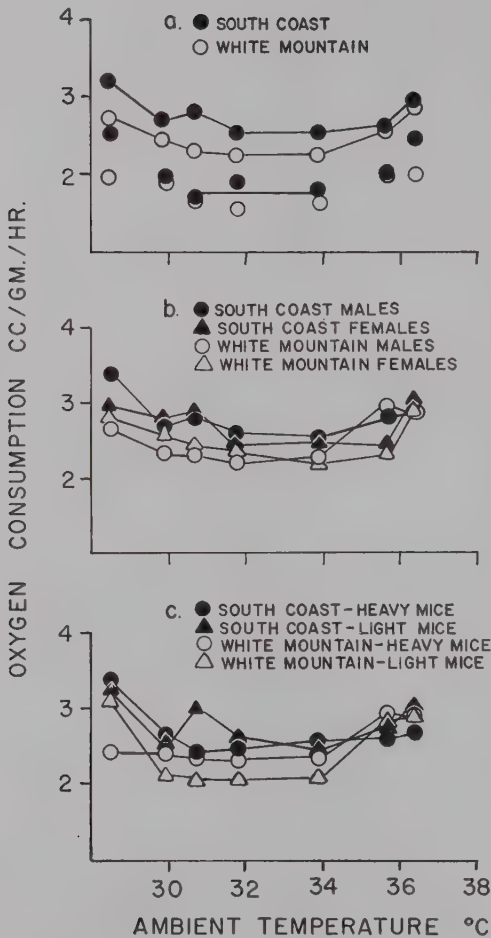


FIG. 3. Oxygen consumption of South Coast and White Mountain mice at 7 ambient temperatures. (a) Means and minima of the 2 groups. The means are connected. Each unconnected point represents the run with the lowest mean value, of each group, at that temperature. Average body weights: White Mountain, 20.8 grams; South Coast, 20.5 grams. (b) Comparison of males and females of the 2 groups. The combined mean body weight of the females is 19.8 grams, of the males, 21.7 grams. (c) Comparison of weight sub-groups consisting of males only. The mean body weights of the "heavy" sub-groups: White Mountain, 22.8 grams; South Coast, 23.9 grams. Mean weights of the "light" sub-groups: White Mountain, 19.2 grams; South Coast, 18.4 grams.

and the median weights are nearly the same for each group.

At all temperatures the White Mountain mean values are below those of the coastal mice, but at the 2 highest temperatures the values converge.

This pattern persists for both sexes and weight groups, in spite of the reversal of the expected weight relationship between the White Mountain sub-groups. At 2 temperatures, 28.5 and 30.7°C, the means differ significantly ($P = .01$), and they approach significance at 2 other temperatures.

The lower critical temperature appears to be between 30 and 31°C. The upper critical temperature is about 34°C. If the metabolic difference between the 2 groups were due entirely to insulation, it would be expected that at some point in the zone of thermal neutrality the curves plotted in Fig. 3 would either cross or merge, but they remain separate throughout this zone. Also, a higher critical temperature would be expected for the mice with the slighter insulation, but this is barely suggested, if at all, in the 3 parts of Fig. 3.

The convergence of values at 35.7° and 36.4° in Fig. 3 must be due to identical reactions and capabilities in heat stress. That the mice were stressed at these temperatures was clear from their behavior. They frequently spread saliva on their fur; sometimes nearly the entire body was wetted. Activity, if present, was in short bursts. Most of the time the mouse lay sprawled on the floor of the cage, sometimes with the tail arched in the air and propped against the wire at some point above the floor. One or more legs were splayed out from the body, and both feet and tail always became very red. A few individuals had convulsive fits, brief periods of jerky behavior, succeeded by quiet periods. Breathing was often shallow, but varied greatly in rate.

To show the full array of variation in oxygen consumption, the results are analyzed by a frequency histogram, Figure 5. The points were calculated by converting each reading in each run at thermal neutrality into its oxygen consumption equivalent. The White Mountain pattern is clearly to the left of that of the South Coast, with a suggestion of a subclustering about 1.7 cc/gm/hr, which is also the predicted basal rate. This sub-cluster, from 1.5 to 1.9, includes 20.3% of the White Mountain readings. Only 3.0% of the South Coast readings fall here. It should be noted that the coastal mice had the greatest range of values and the lowest rate recorded was from a coastal mouse.

The separation of the curves in Fig. 3, especially in the zone of thermal neutrality, could be considered as evidence of an intrinsically lower rate in the high altitude animals. But in neither this experiment nor in Experiment 1 did the mean

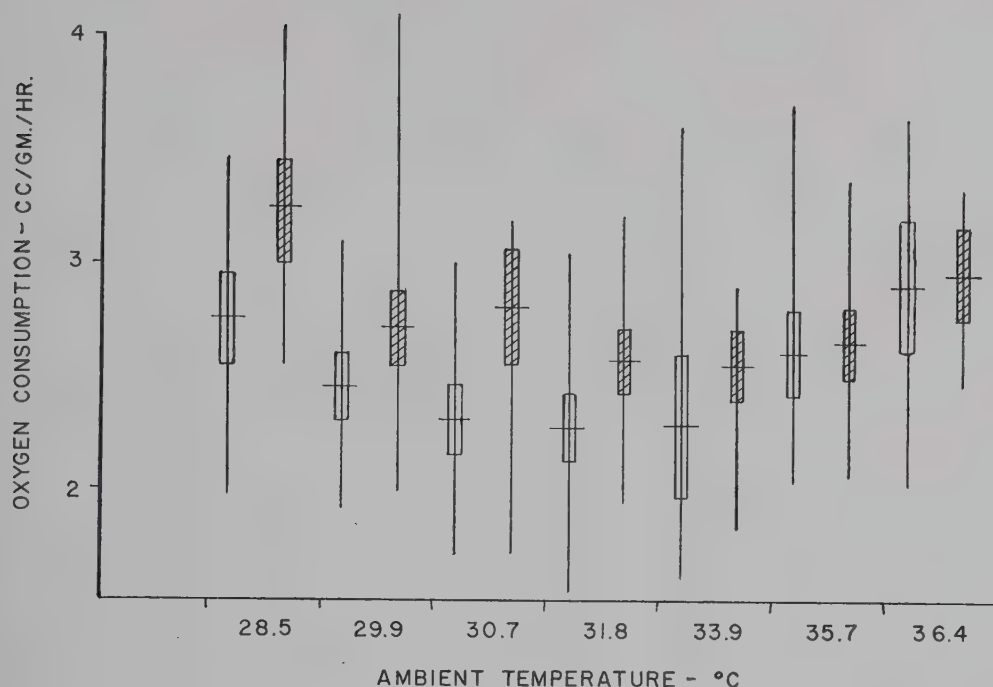


FIG. 4. Variation of rates of oxygen consumption of South Coast and White Mountain groups. Vertical lines represent the range of values at each temperature. Vertical bars represent twice the standard error on each side of the mean. Hatched bars = South Coast; open bars = White Mountain.

values of mountain mice fall appreciably below those expected for an ordinary mammal whose metabolic rate falls on the mouse-elephant curve. Furthermore, the minimum rates of White Mountain and South Coast mice were quite similar at some temperatures (Figs. 3a and 4) although not much statistical weight can be given to this fact. The problem appears to be to understand the relatively high position of the coastal mice, rather than the apparently low position of the mountain mice. From this point of view the results of this experiment can be interpreted as showing that the coastal mice, as a group, spent a greater proportion of test time in an alert or nervous state. From the large range of metabolic rates demonstrated in resting mice (Table II) it is easy to assume that variations in "nervous temperament" would have an important differentiating effect on rates of metabolism.

The relation of metabolic rate and ambient temperature in P. eremicus and P. maniculatus.
Experiment 3.

The procedure for the determination of the metabolic patterns of *P. maniculatus* and *P. eremicus* was identical to that used in Experiment 2,

except that some runs were made at lower temperatures. Nine *P. eremicus* available for this experiment were from Borrego State Park, California, and one was from Death Valley. These mice were of a slightly larger average size than any of the available groups of *P. maniculatus*. Since the metabolic rates of the Mount Rose and White Mountain mice were essentially the same, the heavier individuals of both groups were combined to represent *maniculatus* in this comparison. The mean weights of the 2 groups were: *eremicus*, 24.2 grams; *maniculatus*, 23.0 grams.

The results are plotted in Figure 6. The means of *eremicus* are at or below the level expected for mice of their size, while the *maniculatus* are above this level and in a more irregular pattern. The differences between the 2 groups at 11.1 and 35.7°C and at thermal neutrality are all significant ($P = .01$).

The lower critical temperature of both groups appears to be about 29°C, even though the very low values of *eremicus* at 33°C give the appearance of marking an alternate breaking point of the curve. However, according to the results of Experiment 5, the insulative value of *eremicus* pelage is almost certainly not poor enough to be

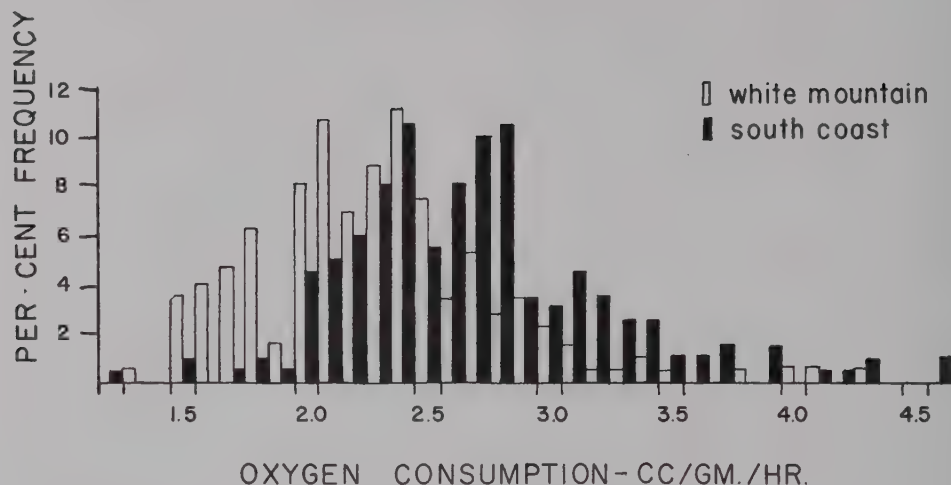


FIG. 5. Frequency distribution of oxygen consumption readings in all runs at thermal neutrality of the White Mountain and South Coast groups of *P. maniculatus*.

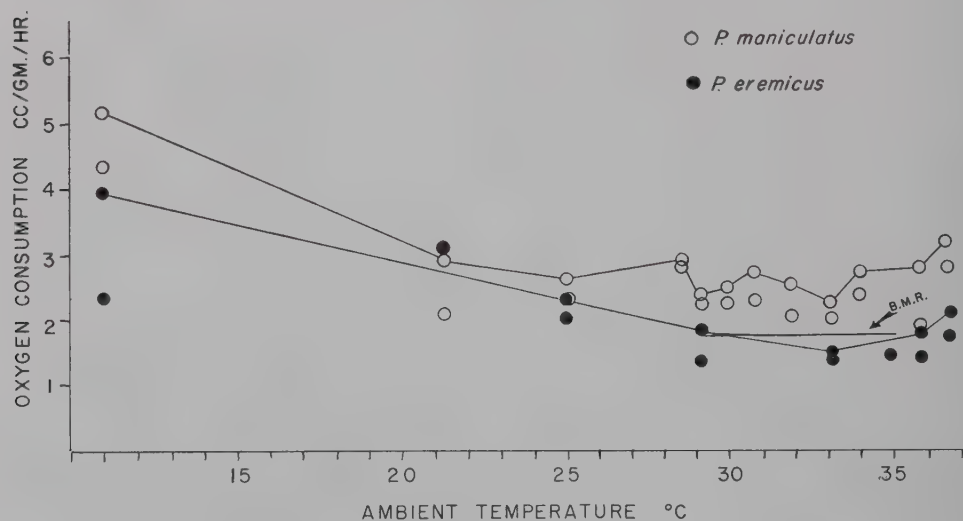


FIG. 6. Oxygen consumption of *P. maniculatus* and *P. eremicus* in relation to ambient temperature. Connected points are group means. Each unconnected point represents the run with the lowest mean value, of each group, at that temperature.

consonant with a critical temperature 4 degrees higher than that of *maniculatus*. Also, the low mean at 33° indicates a rate that is actually below the expected basal level, and should therefore be considered to be a special deviation from the usual curve relating temperature and metabolism. This deviation is probably a response to high temperature.

The upper critical temperature is about 33° for *maniculatus* and close to 35° for *eremicus*.

This upper extension of the zone of thermal neutrality, together with the "sub-basal" position at 33°, is probably correlated functionally with an interesting difference between the groups in their behavior at high temperatures. In only 3 of the regular metabolism runs did individual *eremicus* end the run with a slight dampness of chest or muzzle. In all other tests they remained completely dry. In contrast, individual *maniculatus* often spread saliva on their body surface,

as already described. Two *eremicus* were subjected to high temperature for a longer period than usual; both mice eventually spread saliva copiously. Kangaroo rats, *Dipodomys*, likewise spread saliva reluctantly (Schmidt-Nielsen 1942). The convulsions noted in Experiment 2 were not observed among the *eremicus*.

Below the lower critical temperature the metabolic rate of *maniculatus* increased approximately in proportion to the temperature gradient. The increase in the rate of *eremicus* also appeared to be proportional to the gradient, but the slope was much shallower than expected. At 11° the *eremicus* produced heat at an average rate of of 10.93 kcal/24 hrs, a saving of 2.32 kcal/24 hrs, or 17.5%, in comparison with the heat production of *maniculatus* at this temperature. The following observations show that this difference is correlated with body temperature. Rectal temperatures of 4 *eremicus*, taken at the end of runs at 29°C, averaged 35.4° with a range of 35.1 to 36.6, while the average of 5 *eremicus* at the end of runs at 11° was 33.9° and the range was 29.4 to 36.2. In contrast, the rectal temperatures of 4 *maniculatus*, at the end of 11° runs ranged from 36.5 to 38.2 and averaged 37.2°.

The downward spread of metabolic rates and body temperatures of *eremicus* at 11° suggests incipient torpidity associated with failure of thermal regulation. However, a more likely alternative is that in *eremicus* a relatively low body temperature prevailed throughout the range below thermal neutrality so that the metabolic situation at 11° reflected the consequences of a regulated, although lowered, body temperature. This interpretation is supported by the fact that even at 25° the metabolic rates of *eremicus* were lower than predicted (see Fig. 2).

The low metabolic rate of *eremicus* in general, at all temperatures, might be an expression of an intrinsic rate that is sub-basal in comparison with the typical mammal, or it could result from an extreme passivity in reaction to the experiment. Either of these alternatives would probably entail a reduced body temperature. An attempt was made to measure the relative nervousness of the 2 species by counting fecal droppings accumulated during metabolism tests. Two pairs of runs were made, using the same pair of animals, a male *maniculatus* from Mount Rose and a male *eremicus* from Death Valley. The respective weights of these mice were 29.7 and 31.1 grams. Both were usually quiet during the tests; the Mount Rose mouse was judged to be more restless, on the

basis of head movements and occasional turns. The results are as follows:

Identification	Oxygen consumption (cc/gm/hr)	Number of droppings	Chamber temp. (°C)	Length of run (min)
<i>maniculatus</i> ...	3.08	27	20.3	60
<i>eremicus</i>	3.09	6	"	"
<i>maniculatus</i> ...	2.67	14	24.4	80
<i>eremicus</i>	2.46	4	"	"

In further runs of the same mice, at 4 higher temperatures, the *eremicus* registered a lower average metabolic rate at each temperature. If the dropping count is a valid index of nervous tension, the results indicate a dramatic difference between the 2 mice. In one of the comparisons, however, the large difference in dropping counts is associated with a negligible difference in metabolic rates. This result may be due to failure to separate the dropping accumulation of the one hour adjustment period from that of the time of actual measurement of oxygen consumption. In spite of this uncertainty, the dropping count alone indicates a difference in nervous reaction. Furthermore, direct observations of the individual behavior of all the animals in these 2 groups provides more evidence of such a difference: Individual *eremicus*, with exceptions, settled down quite quickly during the one hour adjustment period and, especially at high temperatures, their more "relaxed" appearance contrasted with the usual attitudes of individual *maniculatus*.

Body temperature. Experiment 4.

The plan of this experiment was to establish the mean and range of body temperatures of the 2 species by methods that would disturb the animals as little as possible. Thermocouples were implanted permanently inside the body so that temperatures could be recorded "from a distance." The procedures were time-consuming so that the number of mice tested was less than anticipated. Nevertheless a considerable amount of data was obtained from each mouse tested. The experiment is especially deficient in that *P. eremicus* is represented by only one individual.

The thermocouples, made of no. 30 copper and constantan wires insulated with 3 thin coats of Copon, were implanted by procedures similar to those described by Bartholomew and Cade (1954). A special modification was necessary to prevent the mice from breaking the projecting wires with their teeth or feet. Each mouse was anesthetized

with sodium nembital injected into the body cavity. An embroidery needle, size 9, was threaded with the constantan end of the thermocouple and inserted through the skin of the dorsal part of the neck and passed between skin and body to a point posterior to the ribs. At this point the needle was forced out through the skin and the wire drawn after it far enough to place the junction approximately at the level of the last rib. The needle was reinserted through the same skin opening and this time forced directly and entirely through the body below the lumbar vertebrae and anterior to the kidneys. The wire was now pulled to lodge the junction next to the vertebrae. The needle was again inserted beneath the skin and the wire drawn forward to emerge next to the copper on the dorsal side of the neck. The result of this operation was a wire loop, one side of copper, the other of constantan, passing beneath the skin and under the vertebral column. The thermocouple was situated essentially in the center of the body and next to the liver and large blood vessels.

One or 2 small glass beads were strung on each wire and cemented to the skin with collodion, and the other skin openings were also sealed with collodion. When the 2 wires were spliced together and trimmed they formed a small "antenna" projecting about an inch above the neck surface. Nearly every mouse tried to remove the wires with its feet, but as long as the splice was intact they stayed in place. In 6 to 10 days the mice appeared to be perfectly healed. Disarrangement of the normal fur surface was negligible. Later autopsies showed no sign of internal damage, with the exception of a peritoneal inflammation in one individual. Data from this individual were rejected.

To record body temperatures the thermocouple wires were unspliced and connected by long leads to a Speedomax, Type G, recording potentiometer. The connection was protected by spun glass tape. The mouse was placed in a glass walled cage with an excess of food and a half apple for water supply. The leads, which hung in a loose spiral above the cage, provided sufficient slack so that the mouse could move to any part of the cage, and were passed through a closed door to the potentiometer. A period of one to 1½ hours was allowed after the initial hook-up for adjustment to the new conditions. The mice were not overly active except for 2 individuals who reacted so violently that they pulled the junction wires clear of the body. Spot observations indicated that the mice were gen-

TABLE VI. Deep body temperatures of individual mice

Designation and temperature	Sex	Weight (g)	Length of run (hr)	T _{amb.} (°C)	T _{mouse} (°C; av. and range)	n
17-27 °C						
<i>P. maniculatus</i>						
White Mountain . . .	F	23.1	5	17.6	37.9 (37.4-38.3)	17
Mount Rose	F	22.6	17.5	21.6	35.9 (34.9-37.6)	89
Mount Rose	M	23.8	11	21.6	36.3 (35.3-37.8)	80
Average					36.7	
<i>P. eremicus</i>						
	F	20.0	16	23.7	36.8 (34.9-38.6)	63
			24	19.8	35.6 (33.3-37.7)	54
Average					36.2	
3.5-9.6 °C						
<i>P. maniculatus</i>						
White Mountain . . .	M	23.7	25	5.2	37.2 (34.2-39.1)	144
Mount Rose	F	19.0	8	9.6	34.7 (32.3-37.1)	93
Berkeley	F	22.8	15	7.3	37.1 (36.0-38.4)	90
Average					36.3	
<i>P. eremicus</i>						
	F	20.0	7	4.7	36.1 (35.1-37.5)	58
			12	6.2	36.8 (34.9-38.4)	87
Average					36.4	

erally quiet throughout each run. One male *eremicus*, available for use as a control, was kept in the refrigerator for 48 hours at an average ambient temperature of 3.7° and subjected to the same conditions as the other mice except that it was not encumbered with an implanted thermocouple and hook-up. Rectal temperatures, taken at the beginning and end of the period were, respectively, 34.2 and 36.6°. These results and the behavior of the mouse were similar in all respects to the pattern shown by the implanted individuals.

The results are presented in Table VI. The mean body temperatures of the 2 species were practically identical. Ranges were nearly as great at room temperatures as at refrigerator temperatures. The grand average of all refrigerator runs differs from the grand average of all room temperature runs by only 0.2°. Therefore, body temperature changes, in the ambient range of the experiment, were independent of air temperature. The minimum temperature recorded from the 5 *maniculatus* tested was 32.3°; the minimum of the *eremicus* was 33.3. The maximums were 39.1 and 38.6 respectively.

The resting body temperature value used in the plotting of Fig. 2 was obtained from the *maniculatus* daytime runs made at room temperature, and represents the combined data from 3 mice: a male and a female from Mount Rose and a White Mountain female.

Sealander's (1953) measurements of esophageal temperatures of *P. leucopus* at room temperature show a higher mean value, but the mean minimum, 36.4°, which he considered to represent the resting temperature, is similar to the mean, 36.7, of the present data from *maniculatus*. Furthermore, the mean of inactive individuals of *leucopus*, measured with deep insertions of a rectal thermocouple by Morrison and Ryser (1959) is 36.2°. The mean of *maniculatus* temperatures in the present experiment is probably a resting value because the runs were long, the mice were relatively undisturbed and they were apparently quiet most of the time. These close similarities between the 2 species, shown by 3 different techniques, is qualified by the fact that Morrison and Ryser (1959) found drastic body temperature declines in some individuals of *leucopus* that were placed in glass jars in water baths of -7° to well above 0°C. Sealander (1953) also recorded sizeable declines in some *leucopus* held without food at an ambient temperature of about 12°. There are striking variations between individuals in the *leucopus* data. Comparable temperature changes were not found in the present experiment, possibly in part because the minimum ambient temperature was above 3°C.

There was a small difference between the means of day and night body temperatures in some of the long runs that included large amounts of both daytime and nighttime. Night was arbitrarily considered to begin at 6:00 P M and end at 6:00 A M. However, for *maniculatus* this differential was slight and in 2 runs the daytime values were actually higher than the night values. These variations may merely be an expression of sampling differences. The *eremicus* values show a larger and more consistent day-night contrast. The following analysis of the long runs illustrates these points:

maniculatus (2 runs; rm. temp.)

$$T_{B(\text{day})} = 36.3 \quad T_{B(\text{night})} = 35.9$$

maniculatus (3 runs; refrig. temp.)

$$T_{B(\text{day})} = 36.5 \quad T_{B(\text{night})} = 36.8$$

eremicus (2 runs; rm. temp.)

$$T_{B(\text{day})} = 36.1 \quad T_{B(\text{night})} = 36.5$$

eremicus (1 run; refrig. temp.)

$$T_{B(\text{day})} = 35.3 \quad T_{B(\text{night})} = 37.0$$

The fact that more clear-cut or consistent diurnal shifts in body temperature were not recorded in these tests should not be considered as proof of the non-existence of such shifts, because the runs did not record equal amounts of day and night. However, it is possible that these animals spend most of their time, even at night, in a resting condition. Especially in cages, the necessary foraging periods are so short that body temperature rises accompanying such activity probably have slight effect on the mean body temperatures for the entire nocturnal period. Furthermore, activity may actually reduce body temperature by disruption of insulation.

The results of this experiment suggest that the body temperature characteristics of *maniculatus* and *eremicus* are not different. However, in the oxygen consumption experiment there was a definite tendency for *eremicus* to decrease its metabolic rate and body temperature, in contrast to *maniculatus*. The average rectal temperature of *eremicus* taken at 11° was 2.5° lower than the average deep body value recorded from the *eremicus* in the refrigerator at an even lower ambient temperature. Conversely the corresponding values for *maniculatus* show the rectal temperature to be higher by 0.9° than the deep body value. These differences are not a result of merely measurement of temperature gradients in the body, because metabolic rates were correlated with rectal temperature differences between the 2 groups. Furthermore, the statistically significant contrast of metabolic rates at 11° supports the reality of the difference shown by the small number of rectal determinations. These results furnish further evidence that in the conditions of these experiments the observed body temperature changes were not simply a function of ambient temperature. They also suggest that the 2 species differed in their behavioral response to the confinement of the oxygen consumption runs in Experiment 3, but did not differ in their responses to the deep body temperature experiment.

Because of the lability of body temperature in *Peromyscus* and other mice, basal metabolism values for these animals must be accepted with reservations. For this reason the data of these experiments cannot be used to decide conclusively whether the comparatively low measured metabolic rate of *eremicus* is a characteristic intrinsic to its cells and tissues or a result of hormonal and nervous regulation. However, the fact that the *eremicus* maintained a deep body temperature that was not lower than that of *maniculatus* when these animals were kept for many hours at low temperatures, is strong circumstantial evidence

for the identity of their intrinsic metabolic capacities.

At ambient temperatures beyond the range studied the species may diverge in their temperature responses. Also, it is possible that in extremes of heat or cold *survival time*, rather than body temperature *per se*, is a more accurate indicator of adaptive capabilities. Hart (1953b) showed that cold-adapted *Peromyscus* do not differ from those acclimated to warm conditions in their levels of metabolism, but rather in the time a given metabolic rate can be maintained in cold air. The morphology of the 2 species is of interest at this point. The sparsely furred ears and long relatively naked tail of *eremicus* might be expected to be more efficient than the well-furred tail and ears of *maniculatus* in conducting and radiating heat away from the body. However, in the high temperature conditions at which heat loss would be helpful, the body-air gradient would be so small that a significant influence on body temperature does not seem likely. On the other hand, at low temperatures, such as are often encountered in *maniculatus* habitats, the *eremicus* tail and ears would be subject to freezing and any heat dissipating superiority they possess would be of distinct disadvantage. In the desert the tail and ears might be of thermoregulatory importance at intermediate "working" temperatures, in the range encountered by nocturnal animals operating at high metabolic rates and away from daytime shelters.

Insulation. Experiment 5.

Direct measurements of the flow of heat through fur were made in order to decide whether the observed differences in metabolic rates could be ascribed to insulation. The pelts used were from non-molting mice and, in most cases, came from mice whose oxygen consumption had been measured a short time previously. The oxygen consumption of some of the mice used in this experiment was not measured, but in all cases the periods of captivity of the individuals of each group were equivalent. A few individuals of *P. leucopus* and *P. maniculatus* from desert areas in New Mexico and some *P. truei* from Berkeley were included in these tests.

A small drum with a thermocouple in its center was made of a thick rubber gasket covered on both sides with discs of fur cut from dried mouse pelts. The thermocouple wires were led through 2 holes in the side of the gasket. In preparing the pelts a standard stretching and drying process was used to minimize variables other than insulation. Each fresh skin was spread, flesh side down, on

a cardboard. The cardboard was placed on a smooth wooden block and a slight tension was exerted on the skin by lightly weighted threads hooked to the nose and each foot and passed over pulleys which were permanently fixed in place on the edges of the block. The pelt was then pinned to the cardboard and allowed to dry in a vertical position.

The fur discs were cut by placing a plastic ring on the flat skin and tracing around it with a sharp scalpel. The diameter of the discs was 4.4 cm. Each drum was constructed with fur samples from 2 mice, since only one disc could be obtained from each pelt. Each pair was chosen at random from the total collection making up each group. The fur samples, forming the 2 faces of the drum, were separated from each other by the width of the rubber gasket, 0.5 cm, and were held in place, with the fur sides out, by thin fiber gaskets. These in turn were clamped down with 2 clips. The hairs were allowed to lie at a relatively flat angle, *i.e.*, not fluffed.

Each drum was placed in a refrigerator and its rate of cooling was measured with a Speedomax, Type G, recording potentiometer. The small size and shape of the drum insured that any internal temperature gradient would be very small. The conductance value of the rubber component was not known and was ignored as a constant. The same gasket was used for all tests. It was assumed that differences in cooling rates of the drums reflected differences in properties of the fur discs. The results provide only an expression of relative insulation values and cannot be used to calculate the conductances of either the dry pelts or the living integument. The procedure used was the same in principle as that of Morrison and Tietz (1957) who measured cooling rates of dead animals and fur-covered casts. The rate of cooling can be expressed as:

$$dT/dt = C(T_B - T_A)$$

The internal temperature of the drum is represented by T_B ; T_A is the ambient temperature; C is the cooling constant which is inversely related to the insulative value of the walls of the drum. Integration and rearrangement of the formula give:

$$C = 2.3 \frac{\Delta \log (T_B - T_A)}{\Delta t}$$

Thus in each test a plot of the logs of $(T_B - T_A)$ in relation to time gave the values needed to calculate the cooling constant. Two, and occasionally 3, runs were made of each drum.

The results, Table VII, indicate that the mean values for the cooling constant are quite similar. None of the differences between the furred drums is statistically significant, except for those between *eremicus* and 4 other groups. These 4 are: North Coast, Mount Rose, Borrego and White Mountain F_1 . All groups are significantly different from the furless drum mean. The group with the poorest insulation, North Coast, differed from that with the best insulation, *eremicus*, by 9.3%. The highest and lowest *maniculatus* values differed by only 7.2%.

TABLE VII. Cooling constants of fur disc pairs from different groups of *Peromyscus*

Designation	Mean cooling constant: hr^{-1}	n	% difference from mean cooling constant of furless discs
Furless discs: bare skins of mountain and lowland individuals of <i>P. maniculatus</i>	12.12 $\pm$.14	6	—
North Coast.....	10.88 $\pm$.32	4	10.2
Mount Rose.....	10.85 $\pm$.36	7	10.4
Borrego. (<i>P. m. sonoriensis</i> , Borrego State Park, Calif.).....	10.80 $\pm$.31	2	10.8
<i>P. leucopus</i> . (Hidalgo Co., New Mexico).....	10.64 $\pm$.39	3	12.2
White Mountain F_1 (lab reared).....	10.61 $\pm$.16	9	12.4
<i>P. truei</i> . (Berkeley, Calif.).....	10.53 $\pm$.42	4	13.1
Berkeley F_1 (lab reared).....	10.17 $\pm$.39	8	16.0
White Mountain.....	10.09 $\pm$.08	2	16.7
<i>P. eremicus</i>	9.86 $\pm$.06	2	18.6

The pelages of *eremicus* measured in these tests may have been representative of the insulation of the animals in their normal desert habitat or they may have changed in response to coastal conditions of the laboratory. In either case the results clearly indicate that in the coastal environment, *eremicus* fur was at least equivalent in insulative effectiveness to the fur of both mountain and lowland forms of *maniculatus*. This naturally suggests the possibility that wild mice of the 2 species may also be similar in insulation or at least that *eremicus* is not inferior in fur growth potential. If such an equality does exist it might be based on the fact that fur has more than one function. These include protection against dirt and abrasion, waterproofing of the skin surface and the provision of a layer of still air to allow some control over insensible water loss. The last may be of great importance in conditions of low vapor pressure, and such conditions are common in both mountain and desert

environments. Also, the range of desert temperatures is wide and efficient conservation of body heat is undoubtedly sometimes of real advantage to the desert mouse.

These data do not give direct information about the fur of the various groups in their natural habitat, but are of use in the interpretation of the oxygen consumption data. The ranking of cooling constants of the *maniculatus* groups does not correlate well with the ranking of metabolic rates (Fig. 2). For example, the F_1 groups were somewhat superior in insulation to the Mount Rose mice, but their resting metabolic rates were much higher. The Berkeley F_1 and White Mountain values for C are practically identical and therefore reinforce the conclusion in Experiment 2 that the separation of the metabolic rates of the mountain and lowland groups was not a function of insulation. The high value of C for the North Coast mice might have been a factor in their relatively high metabolic rates. However, insulation does not appear to have been an important factor in the production of the differences in metabolic rates observed in Experiments 1 and 2.

DISCUSSION AND CONCLUSIONS

The 2 subspecies of *Peromyscus maniculatus* that were studied in detail (Experiment 2) had the same pattern of metabolism, but differed quantitatively at and below thermoneutral air temperatures. This difference was small but consistent. The other experimental groups of *maniculatus*, with the exception of the lab-reared White Mountain mice, could also be separated into either the mountain or lowland category on the basis of metabolic measurements (Experiment 1). These results could not be explained by a subnormal rate of metabolism of the mountain mice. On the contrary, the mountain groups tended to conform well with expectations based on the mouse-elephant curve. It might be argued that, although this conformity is sufficient to show a general similarity to other mammals, the considerable lability of body temperature and metabolic rate in this species could easily obscure small differences in intrinsic metabolic rates. To answer this conclusively it would probably be necessary to measure the oxygen uptake of various tissues of high and low altitude mice, or find a way to control the nervous activity of the whole animal during metabolism measurements. Also, both coastal and mountain groups should be tested under high altitude conditions.

The species is perhaps already pre-adapted to conditions of at least moderately low oxygen

tensions in the sense that the mice carry out their normal life patterns without the necessity of long periods of continual movement or heavy, sustained work. At least in captivity these mice appear to be continually altering their pace; even the nocturnal period of highest activity is broken up by periods of rest or of quiet sensory probing of the environment. An animal on such a daily program would conceivably find no advantage in a reduced tissue demand for oxygen. Instead, the known mechanisms of individual adjustments that bring about acclimation to high altitude, such as increases in red blood cells or myoglobin, might be adequate to meet any competition from genotypes that are less liable to acquire oxygen debts.

Another possibility is that, even though a reduction of the oxygen requirement of one or more body tissues might itself be of some physiological advantage, such a character is not adaptive because it entails a disadvantage, such as lowered body temperature, that reduces its overall value. This particular high altitude character might therefore be selected against.

The evidence indicates that the rather consistent differences in measured metabolic rates between these mountain and lowland subspecies of *P. maniculatus* is not due to different levels of intrinsic metabolism. Nor were the results of insulation measurements (Experiment 5) adequate to explain these differences. The important factor influencing metabolic rate in these experiments appears to be "nervous temperament." This conclusion was inferred mainly from the metabolic evidence and was discussed in Experiments 1 and 2.

The existence of varieties of temperament and behavior in *P. maniculatus* is well known in 2 subspecies: *P. m. gracilis*, the forest deer mouse, and *P. m. bairdi*, the prairie deer mouse. These midwestern forms show definite preferences for forest and grassland, respectively (Harris 1952), and differ significantly in certain traits that have been speculatively related to the physical structure of their habitats (Horner 1954, Foster 1959). For example, *gracilis* is superior in climbing ability and is deliberate in its movements, while *bairdi* is cautious and tends to "freeze" more often when in new situations. The freezing tendency is presumably of value in the relatively open grassland habitat where movement of the prey is an important cue for predators. By analogy, the populations of the present study might have developed behavioral adaptations to certain features of the physical structure of their environment. The mountain habitats are relatively open and often rocky. The coast habitats of California are

typically dense chaparral, broken by openings of various sizes. Different patterns of behavior, with different temperaments associated with them, might be required for success in these 2 types of habitat. McCabe and Blanchard (1950) analyzed a chaparral habitat from this point of view, but at the interspecific level, in their study of 3 species of *Peromyscus*.

Not only were the *P. eremicus* consistently below *P. maniculatus* in metabolic rate, including apparently sub-basal values at some high temperatures, but their thermoneutral zone extended farther into the high temperature zone and they were more passive under conditions of heat stress. The reduction of heat production entailed by these characteristics could, theoretically, be of some advantage. For example, an animal in still air at 35° environmental temperature cannot rely on radiation, conduction or convection to prevent heat storage by the body. In such a situation it can regulate its temperature only by increased evaporation of water from its body surfaces. But, if the animal refrains from this method, while minimizing its heat production, it might still manage a small reduction of the rate of rise of body temperature, and, more important, a small modification of the final body temperature at which body and air are in equilibrium. In the small range of ambient temperatures from the upper critical temperature, about 35° in *eremicus*, to some point lower than the lethal body temperature, perhaps about 42° (Sealander 1953, Dawson 1955) such an animal might avoid a lethal temperature. We have no direct evidence, however, that the reduction of metabolic heat actually has survival value.

The thermoregulatory resources of both species are very limited at temperatures above neutrality. In both there was an elevation of rectal temperatures in metabolism tests at high temperatures. Saliva-spreading is undoubtedly effective, but it can only be classed as an emergency measure. It is evident that the preservation of body water has, in the evolution of *eremicus*, taken precedence over thermoregulation by the expenditure of saliva. The more lavish use of body water by *maniculatus* is perhaps correlated in its evolutionary history with both the relatively infrequent occurrence of above neutral temperatures in its habitat and the availability of environmental water to replace salivary losses. These differences would be expressed only in conditions of heat stress. Not enough is known about the microclimate actually inhabited by either species to allow a guess as to how frequently the conditions of the experiment are encountered by wild populations.

The oxygen consumption data show that in the experimental conditions *maniculatus* expended more energy than *eremicus* and that this difference was associated with a marked difference in nervous temperament. This contrast could have direct adaptive significance. For example, if *eremicus* functions optimally at a lower mean metabolic rate, a possible advantage associated with this trait is the reduction of air flow in the respiratory passages resulting in a decrease in the amount of water lost as vapor. An even greater modification of evaporation may occur in the skin. One cause of increase of evaporation from the skin, at least in *P. m. sonoriensis*, is excitement, accompanied by an elevated metabolic rate (Chew 1955). The physiological mechanism is not known. Water conservation by modifications in either or both of these channels of loss would of course be of special advantage in environments in which low vapor pressures are combined with minimal sources of free water. That some rodent species do differ in insensible water loss has been shown by Chew (1951) and Lindeborg (1955). Another direct correlate of a lower metabolic level is a reduction of the caloric requirement, which in turn might effect the size of foraging ranges, population densities or other adaptations to the availability of food in the different seasons.

Adaptations of the kind just mentioned could be considered as insignificant in relation to the known abilities of mice to survive on sub-normal water rations (Chew 1951, Lindeborg 1952, French 1956, Chew and Hinegardner 1957) or to achieve a constant water intake when diets are changed (Williams 1959). However, survival tests give no direct evidence of reproductive ability and it is reasonable to assume that the populations with the most reproductive success will be those in which individuals have optimal food and water balances. Hence subtle traits that influence these balances might have selective consequences. The geographic relations of the 2 species are of interest in this respect. The distribution of *P. maniculatus* includes extensive desert areas in the southwest United States and northern Mexico, but in extreme Lower Sonoran deserts to which *P. eremicus* is restricted, *maniculatus* is scarce or absent (Osgood 1909). Frequently *eremicus* and *maniculatus* are found in the same desert area, but competition probably tends to separate them into their optimal habitats. For example, Sumner trapped more *maniculatus* than *eremicus* in and near houses at Furnace Creek in Death Valley, whereas in the desert proper *eremicus* predominated (see Grinnell 1937). In the low deserts the physiology and

temperament of *eremicus* might be the decisive factors favoring its success in relation to *maniculatus* in critical seasons or years. Because the annual rainfall in these deserts is extremely variable the amount of desert area mutually occupied by the 2 species may change from year to year.

SUMMARY

Groups of *Peromyscus maniculatus* and *eremicus*, representing 5 subspecies, were trapped in high mountain, lowland and desert habitats. Measurements of oxygen consumption, deep body temperature and pelage insulation were made after these animals had become acclimated to coastal conditions at Berkeley, California.

Among the *maniculatus* groups, the metabolic rates of the mountain mice were more nearly normal when compared with theoretical expectations. The lowland forms metabolized at a higher mean level. These differences appear to be due mainly to differences in nervous temperament. Pelage insulation values did not differ significantly among the *maniculatus* groups. The possibility that in these sub-species temperamental characteristics may be adaptive to the physical structure of the habitat is discussed.

In the comparison of the 2 species, *P. maniculatus* and *P. eremicus*, the *eremicus* were generally more passive and at high temperatures resorted to saliva-spreading less readily than did *maniculatus*. The metabolic rate of *eremicus* was consistently lower than that of *maniculatus*, and near the upper critical temperature the mean metabolic rates of *eremicus* appeared to be sub-basal. Data on pelage insulation in the 2 species suggest that *eremicus* is not inferior in this respect. In ambient temperatures of 3 to 27°C, the deep body temperatures of both species showed wide and similar ranges. In the metabolism tests at 11° the average rectal temperature of *eremicus* was lower than that of *maniculatus*, but in the runs in which deep body temperatures were measured, the mean temperature of the species was nearly the same and fluctuated independently of ambient temperature. The implications of the observed physiological and behavioral differences in relation to geographic distribution is discussed.

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SOME EFFECTS OF FLUCTUATING TEMPERATURES ON METABOLISM, DEVELOPMENT, AND RATE OF POPULATION GROWTH IN THE CABBAGE APHID, *BREVICORYNE BRASSICAE*

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SUMMARY

As a means of dealing with life history data collected at fluctuating temperatures, a weighting function proved valuable for estimating the effective mean temperature during the period of observation. This function,

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based on the rate of oxygen uptake at various constant temperatures, applied to 4-hourly temperatures (from thermograph records) gave a mean value weighted for "biological effectiveness" of the time spent at any temperature.

At constant temperatures the metabolic rate of the cabbage aphid (*Brevicoryne brassicae* (L.)) increased

exponentially from 8 to 30°C then declined rapidly. The rates of aphid development and population increase at normally fluctuating temperatures were investigated in the insectary and fitted to logistic curves. During exponential phases of population growth in the field, the rate of increase plotted against temperature gave a bimodal curve with peaks corresponding to the vegetative and reproductive phases of the host plants. The rate of population increase was maximum at a lower temperature in the field than in the insectary.

INTRODUCTION

When considering the effects of climate on insects we are dealing with the physiological summation of a multitude of environmental factors which interact, reinforcing or opposing one another or acting independently. Since, in the field, populations rather than individuals are dealt with it is necessary to take into account also the effects of crowding, competition, parasitism and dispersal as well as the independent effects of climate on the availability or suitability of food. The last factor is especially important when dealing with highly specialised, obligate plant parasites such as aphids.

In order to study the direct effects of temperature on the cabbage aphid (*Brevicoryne brassicae* (L.)) some of the other variables had to be reduced to reasonable proportions. The first experiments discussed below were therefore carried out in the laboratory and insectary where temperature and several other factors could be more readily measured or controlled. Some field observations are later discussed in terms of these results.

1. Effects of various constant temperatures on metabolic rate

Under warm conditions insects mature rapidly and populations rapidly increase in size. Conversely, under cold conditions insects take longer to reach maturity and population growth is slow. With poikilothermic animals this effect is attributed to the direct action of temperature on metabolic processes and various mathematical equations or empirical curves have been postulated to depict this dependence (Wadley 1936). Since any metabolic process depends upon the interaction of a variety of enzyme reactions with different temperature constants, it is impossible to generalise dogmatically.

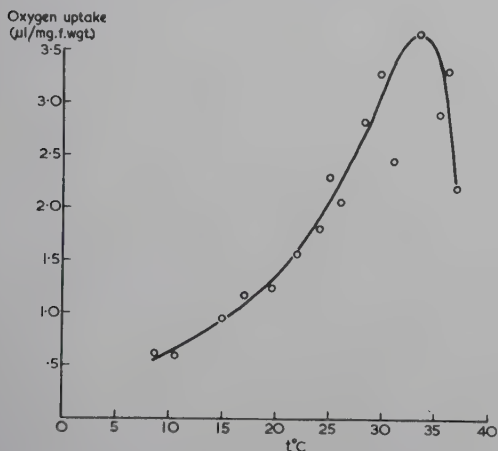


FIG. 1. Rate of oxygen uptake of apterous *B. brassicae* as $\mu\text{l O}_2/\text{mg}$ fresh weight/hour versus temperature.

To provide some basic data on the effects of temperature on overall metabolism, the respiration rate of resting, apterous cabbage aphids was measured at various constant temperatures in Warburg respirometers. The results of a series of experiments are summarised in Figure 1.

Up to about 30°C the aphids consumed oxygen at an increasingly high rate, but above this temperature the respiration rate rapidly declined. Broadbent and Hollings (1951) found that the thermal death point for this species was about 41.0°C while that for *Myzus persicae* (Sulz.) was slightly lower (38.5°C). However, Fenjves (1945) showed that temperatures above 28°C were detrimental for *M. persicae* and inhibited development and reproduction. The above results indicate that metabolic disturbances occur in *B. brassicae* above about 30°C. Measurements were normally carried out for 3 hours but the figures plotted in Fig. 1 represent the mean rate of oxygen uptake for the first hour only. The curve fitted between 8° and 30° is exponential (plotted from regression of log oxygen uptake on temperature). Thus between 10-20° the respiration rate increased 2.2 times. The geometric rate of increase of metabolic rate with temperature is shown more clearly in Figure 2 where the logarithm of oxygen uptake is plotted against temperature.

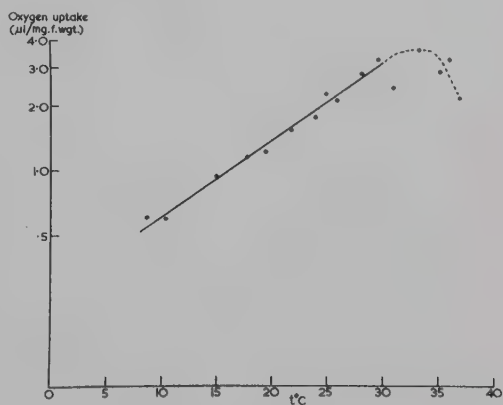


FIG. 2. Log rate of oxygen uptake versus temperature.

2. Effects of fluctuating temperatures on rate of development

From considering the short term effects of temperature on a single physiological process the next step was to consider longer term effects on development of the animal. When investigating the effect of temperature on rate of development the question arises as to whether constant or fluctuating temperatures should be used. Given the necessary apparatus, the use of constant temperatures appears to offer several experimental advantages and indeed many entomologists have undertaken extensive life history studies of aphids under these conditions (e.g. Sanderson 1910, Wadley 1931, Wilson 1938, Fenjves 1945, Bonnemaïson 1951). However, in nature an animal is subjected to diurnal variation of temperature and it has been found that results obtained from constant temperature experiments often cannot be applied directly to the field (Kozhanchikov 1946, Cloudsley-Thompson 1953).

Studies were therefore made of the life history of the cabbage aphid on swede plants (*Brassica napobrassica*

DC) in the insectary at the normal fluctuating temperatures occurring in nature. This work extended over several years and all seasons and thus it was possible to get a series of results with different mean temperatures. The rate of aphid development was taken as the reciprocal of the number of days from birth to the commencement of young production. In Figure 3 these rates are plotted on a logarithmic scale against mean temperature (estimated from daily maximum-minimum temperature readings) for the duration of each experiment. These means were calculated in the usual manner by summing the arithmetical means of the daily maximum and minimum temperature readings and dividing by the number of days observed, i.e.:

$$\bar{t} = \frac{\sum (t_{\max} + t_{\min})}{2d}$$

where $\bar{t}$ = mean temperature
 $t_{\max}$ = daily maximum temperature
 $t_{\min}$ = daily minimum temperature
 d = number of days observed

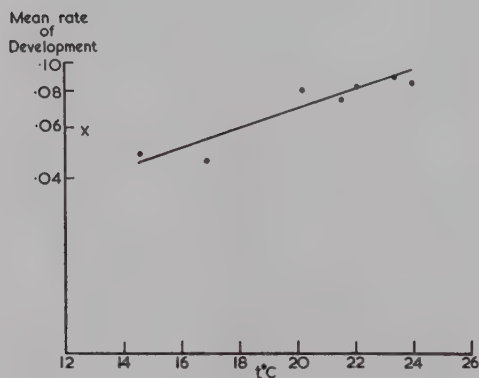


FIG. 3. Rate of development of *B. brassicae* at fluctuating temperatures versus mean temperature.

Over the range of mean temperatures studied the relationship appears to be exponential again. Part of the deviation of experimental values from the expected may be attributed to variation in host composition due to seasonal climatic differences. However, it will be shown below that an important source of error lies in estimation of the mean temperature under fluctuating conditions.

The usual method of estimating the mean temperature is to calculate the mean of daily maximum and minimum temperature readings. However, since diurnal temperature variation does not describe a symmetrical curve of the sine wave type, it is necessary to take into account the time spent at different temperatures. This is commonly effected by integrating the temperature curve and expressing the results as day-degrees (Shelford 1927). Although this type of temperature summation is widely used in ecology it has the disadvantage of assuming that the effects of temperature on animals may be expressed by a linear function (Andrewartha and Birch 1954). We have already shown for the cabbage aphid that this is not the case as at moderate temperatures, at least, the effects of temperature are exponential.

Sanderson (1910) pointed out that temperatures could not be considered additive when calculating thermal con-

stants, and Kozhanchikov (1946) pointed out some dangers in uncritical temperature summation. Cloudsley-Thompson (1953) concluded that it was impossible to use average temperatures for an exact estimation of the influence of weather conditions on the development of insects.

What is needed is a mean temperature weighted for the "biological effectiveness" of the time spent at each temperature. Such a mean temperature was calculated for each of the life history experiments illustrated in Fig. 3 by applying a weighting function (w) based on the metabolic rate curve to the thermograph records. Temperatures recorded at 3-hour intervals were used.

The method of calculating the weighted mean of a series of temperatures is illustrated in Table I. In this case the values for oxygen uptake in Fig. 1 were taken as weights (w) and the weighted mean temperature was found to be 21.1° whereas the arithmetical mean was 25.6°.

TABLE I. Calculation of weighted mean temperature

Observed temperature (t)		Weight (w)	w.t
	10	0.62	6.20
	20	1.40	2.80
	30	3.20	9.60
	33	3.68	121.44
	35	3.47	121.45
Totals	128	12.37	261.49

$$\text{Weighted mean temperature } (\bar{t}_w) = \frac{\sum w.t}{\sum w} = \frac{261.49}{12.37} = 21.1$$

$$\text{Arithmetical mean temperature} = \frac{128}{5} = 25.6$$

When the rate of development was plotted against weighted mean temperature a much better fit was obtained (Figure 4).

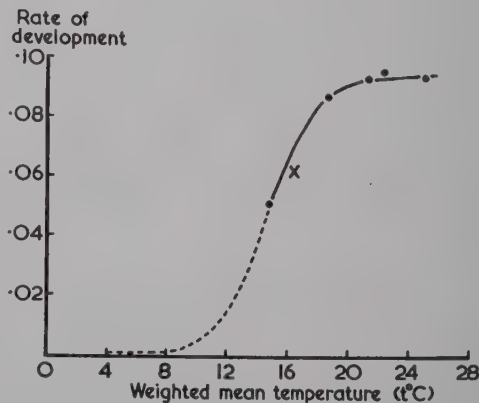


FIG. 4. Rate of development versus weighted mean temperature.

The corrective effect of this transformation is shown well in Figs. 3 and 4 where the value at rate 0.06 (shown by a cross in both figures) appeared to be widely divergent when plotted against its arithmetic mean temperature (Fig. 3) but, when plotted against its weighted

mean temperature (Fig. 4), it fell into line with the other observations for which continuous temperature records were available.

The resulting temperature-development curve is sigmoid in form and has been fitted by eye to the logistic equation below with the aid of logistic graph paper.

$$Y = \frac{0.0927}{1 + e^{(9.2 - 0.625t)}}$$

It is interesting to note that the curve flattens off in the vicinity of 22°C (72°F)—a lower temperature than might have been expected from earlier respiration studies. It suggests that some host factor (such as food supply) may have been limiting. For this reason the logistic function was used. In the above equation 0.0927 is the theoretical maximum rate of development, 0.625t is the rate of development and 9.2 is a constant.

3. Effects of temperature on rate of population growth

From studying the effects of temperature on individual aphids, let us now consider the effect of normal fluctuating temperatures on the rate of population increase. With cabbage aphids on swede plants in the insectary, the rate of population growth has been found to be exponential as a rule for several weeks. Under these conditions of unlimited growth the rate of population increase may be calculated from the expression:

$$N_t = N_0 e^{r't}$$

Where N_0 = number of aphids at time zero

N_t = number of aphids at time t

r' = rate of increase

e = base of Napierian logarithms

The value of r' was determined from linear regression of log number of aphids on temperature for a series of experiments and plotted against mean temperature (determined from daily maximum and minimum temperature readings) (Figure 5).

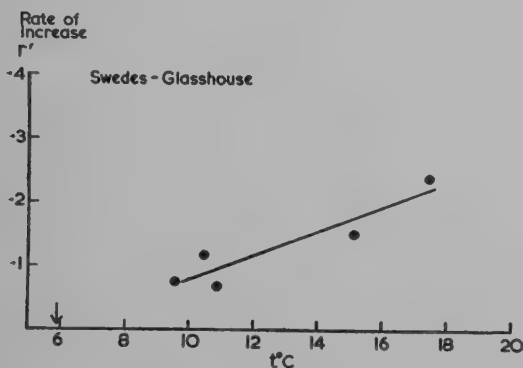


FIG. 5. Rate of population increase (r') versus mean temperature (insectary).

Unfortunately thermograph records were not available for this series of experiments so weighted mean temperatures were not calculated. Nevertheless, it is interesting to note that the rate of increase would theoretically become zero at 5.9°C (bearing in mind the dangers of extrapolation). This is in the vicinity of the expected value from Fig. 4.

The statistic r' has been considered above as an empirical constant but it has an obvious affinity to the

"intrinsic rate of increase" r_m of Lotka which has been applied to insect populations by Birch (1948) and others. Life tables were drawn up from another set of insectary experiments and the intrinsic rate of increase was calculated. The values of r_m obtained in three independent experiments are shown in Table II.

TABLE II. The intrinsic rate of increase (r_m) of *B. brassicae* at fluctuating temperatures (calculated from life tables)

Mean temperature (from max-min readings) °C	Weighted mean temperature °C	Intrinsic rate of increase: r_m
20.1.....	18.9	0.230
24.6.....	21.6	0.233
21.7.....	21.6	0.235

The results of Fig. 5 and Table II were combined in the logistic equation: $Y = \frac{0.236}{1 + e^{(6.0 - 0.5t)}}$ which is shown

graphically in Figure 6.

These results indicate that comparable results were obtained whether the rate of increase was estimated empirically or from life table data—though some improvement of fit might have been expected if weighted temperature means had been available.

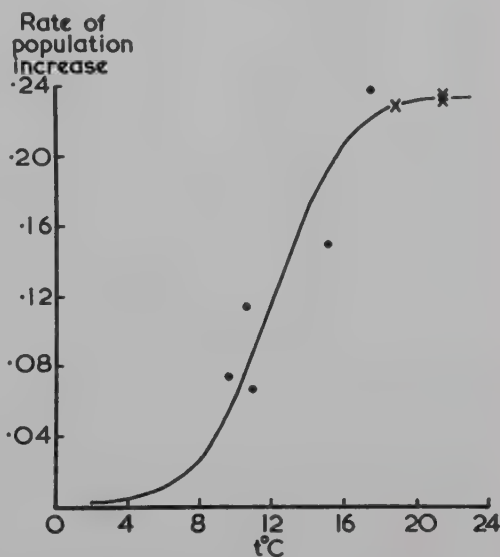


FIG. 6. Logistic curve of rate of population increase versus mean temperature ($\bullet = r'$; $\times = r_m$).

The results so far discussed indicate that the metabolic rate, rate of development and rate of population growth are functionally related to temperature: metabolic rate in an exponential form and the others in a logistic manner. To what extent can this be applied to field results?

In the course of a study of the ecology of the cabbage aphid in Canterbury, New Zealand (Lamb and Lowe, in

preparation) weekly samples were taken of aphid populations on replicated trials of 3 species of field crop brassicas at 3 different sites in 1958-59. From these results some values were calculated for the rate of population increase on each host species. One of the restrictions on the use of r' is that it assumes a geometric rate of increase in an unlimited space. The values of r' were therefore calculated only when these conditions were apparently fulfilled for 3 or more successive weeks. Some values for r' plotted against mean (unweighted) temperature are shown in Figure 7.

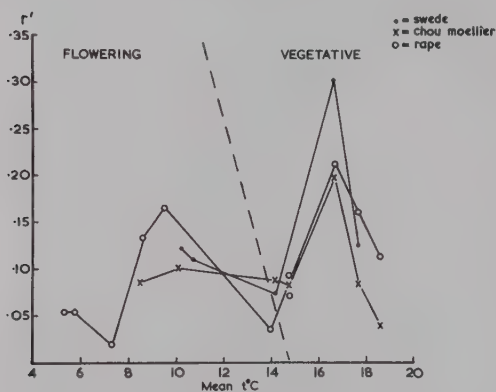


FIG. 7. Rate of population increase of *B. brassicae* on 3 species of brassicas in the field (● = swede; x = chou moellier; o = rape).

When the host plants were in the vegetative stage of growth (right hand side of Fig. 7), the rate of increase reached a maximum at 16.7°C on each host variety and then declined. This effect appeared to be independent of site, host variety or time of sampling. However, when the plants were in the flowering stage a second peak occurred at about 10°C when the rate of aphid increase was greater than expected from results obtained in the vegetative stage. This is readily explained by the enhanced aphid suitability of brassicas in the flowering stage. During flowering and seed formation the flower stalks of these biennial plants are the site of intense phloem translocation and this is reflected by dense aphid populations at the distal ends of the stalks. The reproductive powers of aphids and other phloem feeding insects are greatly affected by the quantity and quality of food available to them (Kennedy and Stroyan 1959). *B. brassicae* can barely survive and reproduce on shepherd's purse (*Capsella bursa-pastoris* (L.)) in the vegetative stage but the aphids will multiply vigorously on flower-heads of this plant.

CONCLUSION

The mean temperature at which the rate of population increase was maximum in the field (16.7°C) was considerably lower than the comparable maximum estimated from insectary experiments (22°C). In both cases the maximum was much lower than temperatures which respiration experiments indicated might have been directly deleterious to the aphids. One factor limiting the rate of development of an animal is the quantity and quality of food available to it. Plants raised in the glasshouse grow more rapidly and have a wider spectrum of highly suitable leaves for aphids than plants grown outdoors. Kennedy, Lamb and Booth (1958) and Ken-

nedy and Booth (1959) have demonstrated that physiological changes in host plants induced, by environmental factors such as water stress, have marked effects on suitability for aphid infestation. It is therefore suggested that the nutritional conditions imposed by the physiological condition of the host plants have a limiting effect on the temperature dependent rate of aphid development and rate of population growth and that this effect is more marked in the field than in the insectary. In the field it is of course necessary to take into account other factors. These will be discussed elsewhere (Lamb and Lowe, in preparation).

The above results indicate that the effects of temperature on insect metabolism, growth rate and rate of population growth are exponential over a moderate range of temperatures but, where other external factors result in limiting conditions, the relationship is quite well described by the logistic curve. The use of temperatures weighted for "biological effectiveness" gives a substantial improvement in fit for experimental data and such weighted mean temperatures should have wide application in biological studies where appropriate weighting functions can be justified.

This does not imply the day-degrees hyperbola of Simpson (1903) and Sheldon (1927) should be abandoned in practical work. Indeed the work of Bodenheimer (1958), for example, has demonstrated the value of this relationship in field ecology. We must, however, agree with Andrewartha and Birch (1954) that the hyperbola gives only a fairly rough approximation of the effects of temperature on rate of development. For many purposes this is probably adequate.

It has often been suggested that fluctuating temperatures have some special stimulating effect on insect development when compared with constant temperatures. Cloudsley-Thompson (1953) has summarised a diversity of papers on this subject. Many of the difficulties raised by earlier workers can be resolved by examining their methods of estimating mean values for fluctuating temperatures. A further possible source of error must be considered with phytophagous insects raised at constant temperatures and that is quality of their plant food. Without the use of special equipment ("phytotrons") it is not easy to raise vigorous plants under constant temperature conditions with adequate light. The chemical composition of plants depends to a great extent upon the conditions under which they are raised and this will influence insects feeding upon the plants. Further, one must be sure that the artificial environmental conditions do not have undesirable effects on the insects (other than those being studied) e.g. through abnormal radiation or evaporation.

Nevertheless, we cannot dismiss the possibility that constant temperatures may have direct, undesirable effects on insect metabolic processes. This point still remains not proven.

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NUTRIENT DEFICIENCIES IN TWO BITTERBRUSH SOILS

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INTRODUCTION

The range of bitterbrush, *Purshia tridentata* (Pursh.) DC and *Purshia glandulosa* Curran, covers about 340,000,000 acres in the 11 western range states and southern British Columbia. *P. glandulosa* is limited to a small section of the Southwestern portion of this area and ranges into Baja California, Mexico.¹ It is one of the most important range browse plants in the West (Hormay 1943). The soils upon which it grows have been studied very little.

This investigation extends some work begun in 1955 on the effect of environment on the early growth of bitterbrush and reported by Wagle (1958). The nutrient status of several bitterbrush soils was determined in this study by lettuce, other indicator plants, and bitterbrush seedlings, and used to interpret environmental effect on plant establishment.

This paper describes the growth responses of bitterbrush seedlings over 2 yrs in 2 types of bitterbrush soils under different nutrient treatments. The responses are compared to some of the original standard pot tests in which Romaine lettuce seedlings were used.

¹ This area estimate is based on figures given in Hormay (1943) for *P. tridentata*. His figures were based on information obtained from the U. S. Forest Service, Region 5 and the Division of Dendrology and Forage Investigations, U. S. Forest Service, Washington, D. C. The range for *P. glandulosa* is about 1,000,000 acres in California (Nord 1959) and the total distribution is probably less than 2,000,000 acres.

MATERIALS AND METHODS

The *P. tridentata* and *P. glandulosa* seeds used in these tests were obtained on the east side of the Sierra Nevada. The *P. tridentata* seeds were collected north of Janesville, California, at an elevation of 4,400 ft and close to 40° 15' N. Lat. The *P. glandulosa* seeds were collected near Bishop, California at an elevation of 5,500 ft, near 37° 45' N. Lat. *P. glandulosa* was not used as an indicator plant in both soils because of a limited seed supply.

The method used to determine soil fertility is a modified Mitscherlich technique which utilizes Romaine lettuce as an indicator plant. In California, several hundred soils have been surveyed by this method. Correlations have been made between greenhouse and field plot data which now make it possible to anticipate field responses from pot test data (Jenny *et al.* 1950).

The procedures given for lettuce were modified to provide a larger container for growing bitterbrush plants over a fairly long time.

The lettuce tests were set up in 6 in. pots using 1600 g of soil sieved through a half-inch mesh. Nutrient conditions were compared in triplicate for each soil as follows:

1. Control series, no nutrients added,
2. + N + P + KS series,
3. - N + P + KS series,
4. + N - P + KS series, and
5. + N + P - KS series.

Nitrogen (N) was added at the rate of 200 lbs/acre as ammonium nitrate, phosphate (P_2O_5) at 300 lbs/acre as mono-calcium phosphate, and potassium (K_2O) at 200 lbs/acre as potassium sulfate. In establishing these rates, it was assumed that an acre of soil to a depth of 7 in. weighs 2 million pounds.

Ten-inch pots were used for the bitterbrush tests. Five seedlings were planted in 6400 g of soil in each pot. The treatments and rates of application were the same as in the lettuce tests except that the bitterbrush tests were made in duplicate.

All pots were painted on the inside before using with 2 coats of black asphalt paint and on the outside with aluminum paint. The chemically pure nutrient solutions were thoroughly mixed in the soils. The soils were irrigated with distilled water when necessary.

SOIL DESCRIPTIONS

The 2 soils used were collected on the east slope of the Sierra Nevada. One sample was from the Flukey Springs Experimental Area, of the Pacific Southwest Forest and Range Experiment Station, elevation 4,250 ft, Lat. $41^{\circ} 39' N.$, Long. $121^{\circ} 14' W.$ Annual precipitation averages between 12 and 14 in., much of it falling as snow. Climatic records of the U. S. Forest Service show that temperatures are moderate and summer maximums are usually less than $100^{\circ} F$ while below freezing minimums may prevail into the month of July. The surface varies from flat to rolling; it is covered with trees and shrubs and is underlain by basaltic rocks of volcanic origin. The soil in the experimental area is several feet deep, and at the surface is a reddish brown loam, friable and soft, and is visibly high in organic matter. It is moderately permeable, and slightly acid to neutral (pH 6.0-6.3 in the 6 in. surface

TABLE I. Vegetation found on two soil sites near the Flukey Springs Experimental Area^{1, 2, 3}

Species	QUARANTINE STATION El. 4,300 ft.		FLUKEY WELL El. 4,250 ft.	
	Cover %	Composition %	Cover %	Composition %
Perennial grasses.....	4.7	22.9	2.5	16.9
Perennial forbs.....	0.1	0.4	T	T
Woody shrubs				
<i>Purshia tridentata</i>	13.6	66.1	2.5	16.9
<i>Artemesia tridentata</i>	0.7	3.2	5.8	38.3
Others.....	1.5	7.4	4.2	27.9

¹ Vegetation data furnished by Dr. E. C. Nord, U. S. Forest Service, Division of Range Management, Pacific Southwest Forest and Range Experiment Station, Berkeley, Calif.

² Soil and vegetative cover on these sites are comparable to those found on the soil collection area.

³ A large number of dead *P. tridentata* plants were observed on the Flukey Well site.

layer to 7.0 at a 5 ft depth). The soil has developed from the weathering of the underlying basaltic rocks. Natural woody vegetation in the area is made up of *P. tridentata*, juniper (*Juniperus occidentalis* Hook.), ponderosa pine (*Pinus ponderosa* Lawson), big sage (*Artemesia tridentata* Nutt.) and a few rabbit brush plants (*Chrysothamnus parryi* Greene). The understory is composed of perennial grasses, and forbs (Table I). This area has not been mapped but this soil closely resembles what has been described elsewhere as the Underwood soil series

The second soil was collected north of Bishop, Calif., near the summit elevation sign on Deadman Summit on the east side of Highway 395, elevation 8,041 ft, Lat. $37^{\circ} 46' N.$, Long. $119^{\circ} 01' W.$ Climatic records are not available but the writer's experience in and near the area indicates the climate is similar to that given above, except that annual rainfall may be slightly higher and temperatures more extreme. This soil has a very coarse texture and is almost a pure pumice. A pH of 5.6 was measured in the surface 6 in. The vegetation was sparse, with wide, open areas of bare soil. The woody plants were mainly a mixture of *Pinus jeffreyi* Murr. and *Purshia tridentata* (Pursh) DC. The understory consisted of a few widely scattered clumps of grasses and occasional forbs (Table II).

TABLE II. Vegetation found on two pumice soil sites in California^{1, 2, 3}

Species	CRESTVIEW El. 8,200 ft. Lat. $37^{\circ} 47' N.$ Long. $118^{\circ} 59' W.$		OLD MONO MILLS El. 7,900 ft. Lat. $37^{\circ} 49' N.$ Long. $118^{\circ} 59' W.$	
	Cover %	Composition %	Cover %	Composition %
Grasses:				
<i>Stipa occidentalis</i>	T	T	T	T
<i>Silvanian hystrix</i>	T	T	T	T
<i>Carex</i> sp.....	0.4	2.3	0.6	5.5
Woody Shrubs:				
<i>Purshia tridentata</i>	12.5	72.1	8.2	76.0
<i>Pinus jeffreyi</i> (shrub size)....	4.2	24.3	1.8	16.6
Others.....	0.2	1.2	0.2	1.8

¹ Vegetation data furnished by Dr. E. C. Nord, U. S. Forest Service, Division of Range Management, Pacific Southwest Forest and Range Experiment Station, Berkeley, Calif.

² The soil and vegetation on these sites are comparable to those found in the vicinity of the Deadman Summit soil collection area. Jeffrey pine of tree size forms a scattered open overstory.

³ N. E. A. Hinde in his "Evolution of the California landscape" California Division of Mines Bulletin 138, December 1952, provides an interesting commentary on the geology and origin of these soils.

EXPERIMENTAL RESULTS

Table III gives the dry weight yields of lettuce shoots and *P. tridentata* and *P. glandulosa* shoots and roots grown in the Flukey Springs soil in absolute gram weights. Figure 1 gives the yields relative to the full fertilizer treatment. Although

TABLE III. Dry weights of plants grown in the Flukey Springs soil

SHOOTS			
Nutrient Combination	Lettuce	<i>P. tridentata</i>	<i>P. glandulosa</i>
	gms.	gms.	gms.
Check.....	0.3	70	57
NPKS.....	6.3	130	159
PKS.....	2.7	119	110
NKS.....	0.2	61	45
NP.....	6.5	122	122

ROOTS			
Nutrient Combination	Lettuce	<i>P. tridentata</i>	<i>P. glandulosa</i>
Check.....	NOT DETERMINED	39	21
NPKS.....		74	35
PKS.....		58	29
NKS.....	DETERMINED	53	18
NP.....		60	29

Lettuce Flanted: Sept. 1956 *P. tridentata* Planted: May 1958
 Harvested: Oct. 1956 Harvested: July 1960
 P. glandulosa Planted: May 1958
 Harvested: Aug. 1960

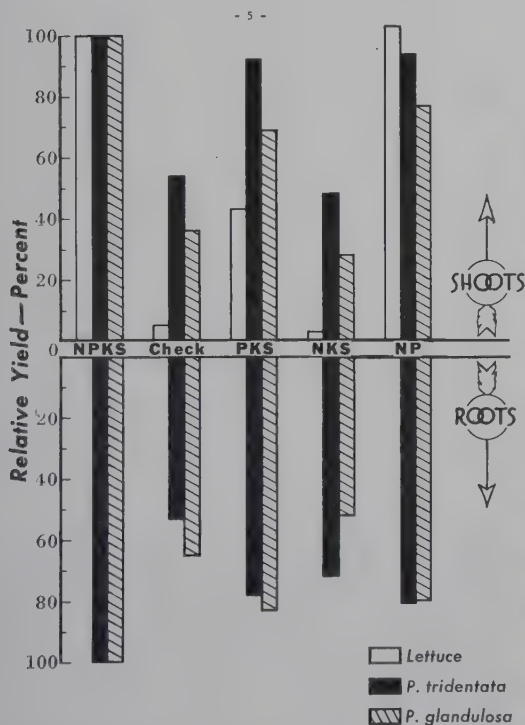


FIG. 1. Relative yields for the plant indicator species used in the Flukey Springs soil.

absolute yields vary considerably with season, the relative yields are much less variable (Jenny *et al.* 1950).

The control and $-P + NKS$ results show that phosphorus is the most limiting nutrient on shoot growth in *P. tridentata*, *P. glandulosa* and lettuce plants (Figs. 2 and 3). Root growth in *P. tridentata* and *P. glandulosa* is not greatly affected by the omission of phosphorus.

The yield for lettuce shoots in the $-N + PKS$ treatment indicates that nitrogen should also be a limiting nutrient on plant growth in the Flukey Springs soil. However, *P. tridentata* shoot growth in the $-N$ treatment was good. It was comparable to that obtained with a full treatment ($+NPKS$). *P. glandulosa* shoot growth too was greater than would be expected with this treatment. Possibly the roots of the bitterbrush plants in this soil obtained atmospheric N from their numerous root nodules (Fig. 4). Such nodules were first reported by Wagle (1958). They contain a fungus which has been tentatively identified as an actinomycete by Dr. R. V. Bega, Plant Pathologist, Pacific Southwest Forest and Range Experiment Station, Berkeley, Calif. This nodular organism is symbiotic and may be involved in fixing atmospheric N in a form available to the host.

Table IV gives the dry weight yields of lettuce

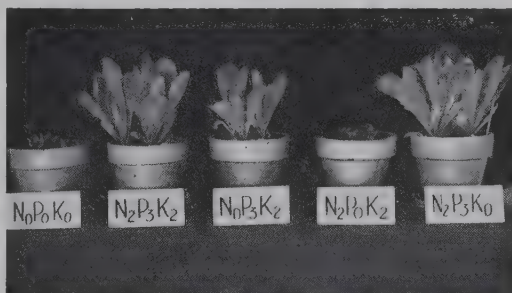


FIG. 2. Growth of Romaine lettuce indicator plants in the Flukey Springs soil after treatment with different combinations of nutrients.

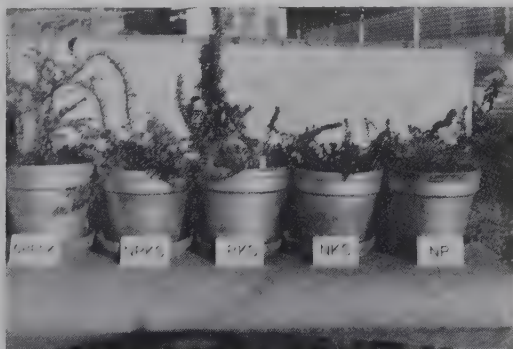
FIG. 3. Growth of 2 yr *P. tridentata* seedlings in the Flukey Springs soil after treatment with different combinations of nutrients.



FIG. 4. Root nodule of *P. tridentata*. Other nodules are present in the root mass at the top of the figure.

TABLE IV. Dry weights of plants grown in the Deadman summit soil

Nutrient Combination	SHOOTS		ROOTS	
	Lettuce	<i>P. tridentata</i>	Lettuce	<i>P. tridentata</i>
	gms.	gms.	gms.	gms.
Check.....	0.3	14	NOT	17
NPKS.....	3.5	68		76
PKS.....	0.3	11	DETER-	15
NKS.....	1.5	56		75
NP.....	2.0	62	MINED	52

Lettuce Planted: Sept. 1956 *P. tridentata* Planted: May 1958
Harvested: Oct. 1956 Harvested: June 1960

shoots and *P. tridentata* shoots and roots in absolute gram weights, and Figure 5 gives the relative per cent yields for the Deadman Summit soil. In this soil the bitterbrush yields in general parallel the lettuce yields, except that the $-P + NKS$ and $-KS + NP$ yields are much higher than might be expected on the basis of lettuce results alone (Figs. 5 and 7). The difference in lettuce yield between the $-KS + NP$ and $+NPKS$ treatment in the Deadman Summit soil was diagnosed visually as a sulfur deficiency rather than a potassium deficiency (Figs. 5 and 6). This was verified by a supplementary test comparing sodium sulfate and potassium chloride in addition to a $+NP$ treatment. The results indicate that the bitterbrush plants either have less need than lettuce for

phosphorus and sulfur or are more efficient in obtaining these elements from the soil.

Nitrogen is definitely indicated as the most limiting nutrient in this soil on the basis of both lettuce and bitterbrush yields (Table IV and Fig. 5). A significant difference between the bitterbrush plants grown in this soil and the plants grown in the Flukey Springs soil is that no

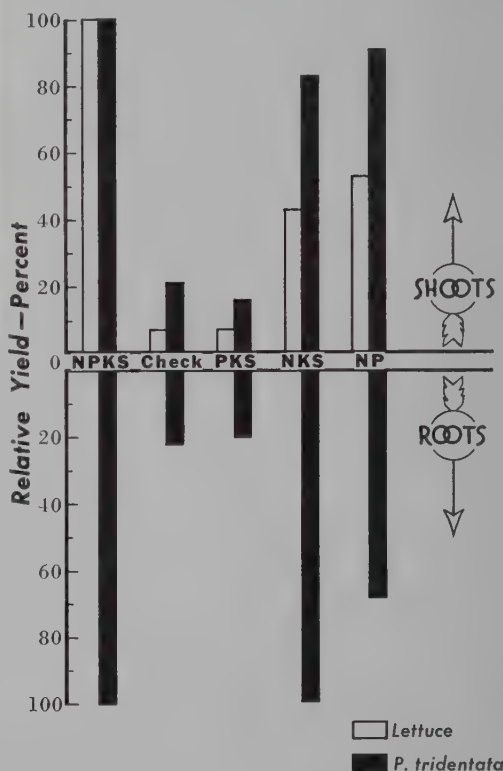


FIG. 5. Relative yields for the two plant indicator species used in the Deadman Summit soil.



FIG. 6. Growth of Romaine lettuce in the Deadman Summit pumice soil after treatment with different combinations of nutrients.



FIG. 7. Growth of 2 yr. *P. tridentata* seedlings in the Deadman Summit pumice soil after treatment with different combinations of nutrients.

nodular growths were found in the roots of any of the bitterbrush plants in the Deadman Summit soil. This difference appears to support the suggestion that the root nodules found on bitterbrush plants grown in the Flukey Springs soil have a nitrogen fixing ability.

Root yields for *P. tridentata* (Table II and Fig. 5) indicate nitrogen is also the most limiting nutrient to root growth in the Deadman Summit soil.

On the basis of the lettuce tests which indicated sulfur as a nutrient deficiency, the depressed root yield obtained in *P. tridentata* under the —KS +NP treatment may be attributed to a sulfur deficiency (Fig. 5). The sulfur deficiency indicated for the Deadman Summit soil did not limit shoot growth in *P. tridentata* but appeared to slightly limit root growth.

CONCLUSIONS AND DISCUSSION

Romaine lettuce can be used as an indicator of nutrient deficiencies for wildland or uncultivated soils with the following reservations:

1. Growth responses of plants naturally growing in the soils to be tested should be correlated with the lettuce growth responses. Vlamis, Stone and Young (1954) used a field rating method of correlating nutrient status of a soil with the cover density of the native vegetation. They found that the soils producing the best yields of dry matter in the lettuce pot tests also had a high density in native chaparral cover. Vlamis, Schultz and Biswell (1959) correlated the nutrient status of 3 soils by pot tests with lettuce and native plants consisting of *Pinus ponderosa*, *Ceanothus integerrimus*, *Adenostema fasciculatum*, and *Cercocarpus betuloides*. Wagle (1958), determining the nutrient status of several different bitterbrush soils, used a number of different methods. Lettuce pot test results were positively correlated with numbers of bitterbrush plants per unit area, the germination and early growth of bitterbrush under different soil conditions, field plantings of bitterbrush and mechanical and other soils analyses. The evidence from these studies indicates that, as correlations between wildland plant growth responses and indicator plant growth responses accumulate, bioassays of wildland soils using indicator plants will give additional information on soil nutrient deficiencies which may be useful in the manipulation of vegetative cover with respect to volume of growth and species composition.
2. The requirements of lettuce for the various nutrients used in the pot tests of this study are probably higher than the requirements of many native wildland plants. Wildland plants may actually need less of these nutrients or may be more efficient in obtaining them from the soil. Studies by Vlamis *et al.* (1954), Vlamis *et al.* (1959), Crocker and Major (1955), Helmers *et al.* (1955), Helmers and Kelleher (1959), Rennie (1955), Krause (1958), Wagle (1958), Kruckeberg (1954), Quick (1944), Whittaker (1954) and others seem to support either one or the other of these premises. Stebbins (1950) cites an example in the genus *Hutchinsia* of a form growing on limestone which has a higher calcium requirement than other plants of the same species not growing on limestone.
3. Plant indicators such as Romaine lettuce, barley, or tomato seedlings may not give a true picture of nitrogen deficiencies in relation to some native plants. The studies by Bond (1955), Bond and Scott (1955), Bottomley (1915), Helmers and Kelleher (1959), Vlamis *et al.* (1954, 1959), Quick (1944), Schwartz (1959), and Wagle (1958) indicate that various wildland brush species with their associated symbiotic organisms are capable of fixing atmospheric nitrogen for plant use or of altering the soil conditions so that this process can be carried on more efficiently by other soil organisms. The species so reported generally have nodulated roots which might indicate the presence of a symbiotic organism. Schaefer (1943) and Schwartz (1959) state that symbiosis involving actinomycetes has been found in 7 genera (*Alnus*, *Casuarina*, *Ceanothus*, *Coriaria*, *Eleagnus*, *Hippophae* and *Myrica*) and that the organs of symbiosis are nodules on the roots. Gardner and Bond (1957) found evidence of a similar symbiotic relationship in nodulated plants of *Shepherdia*. Schoenike (1958) gives some in-

direct evidence that indicates the presence of a nodular symbiont in the genus *Dryas*. Von Ploto (1940) found that an actinomycete isolated from the root nodules of alder utilized atmospheric nitrogen in culture. Hiltner (1896) and Nobbe and Hiltner (1904) succeeded in cultivating nodule bearing alder (*Alnus glutinosa*) and sea buckthorn (*Hippophae rhamnoides*) in nitrogen free media. Bond (1955) found in an isotopic study that nitrogen fixation was associated with nodules in *Alnus*, *Myrica*, and *Hippophae*. Krebber (1932), in a series of careful investigations, found that alder with its symbionts is capable of using atmospheric nitrogen. Raup (1941) suggests that N fixation, possibly associated with nodules of *Shepherdia* may be of special ecological significance in boreal areas.

Field observations made in the Flukey Springs area in 1956 indicated that many *P. tridentata* plants growing naturally in the area were dying out. Drouth as a factor in this soil and climate is unlikely (Wagle 1958). The present study indicates that soil nutrients could be at least partly responsible for this in the following ways:

1. Phosphorus was the most limiting nutrient on bitterbrush shoot growth in the Flukey Springs soil samples. Wagle (1958) previously found that in a soil having a dense cover of healthy, reproducing *P. tridentata* plants the macronutrients (NPKS) tested for were available to lettuce plants in a well balanced ratio (relative yields were 60% for —N, 46% for —P, and 60% for —KS). The low phosphorus supply in the Flukey Springs soil is fairly typical of soils derived from basic igneous rocks. This condition may be further aggravated by a progressive degradation over the years which could be due to leaching, cropping by man or livestock and game, fire, or combinations of these. The dying out of bitterbrush plants may be one of the ecological changes resulting from this process of soil degradation. The use of phosphate soil amendments in the Flukey Springs area would test this hypothesis and might increase bitterbrush plant density in the area. Beadle (1954) presents some data which indicate that soil phosphate may play an important role in delimiting plant communities in Australia.
2. Bitterbrush plants grown in the Flukey Springs soil samples acquired root nodules and appeared to be able to increase the supply of available nitrogen. Helmers and Kelleher (1959) found that plants of *Ceanothus leucodermis* Greene,

a plant having root nodules similar in appearance to those on bitterbrush roots, removed more nitrogen from the soil than was originally present. In addition, these plants left almost twice as much available nitrogen in the soil for subsequent usage. Perhaps bitterbrush plants growing in the Flukey Springs area may be changing their environment by increasing the available soil nitrogen. This soil change alone, or together with the effect of a low phosphorus availability, may favor the increase of other plants with different nutrient requirements at the expense of the existing bitterbrush plants.

Field observations were made in 1956 on plant density in the Deadman Summit area. The area is characterized by large open areas of loose exposed pumice soil with scattered trees and shrubs. *P. tridentata* plants were widely scattered and individual plants were generally small and poorly formed. This study indicates *P. tridentata* plant density and growth or both might be increased by soil treatment as follows:

1. Nitrogen was the most limiting nutrient in the soil samples from the area. Helmers and Kelleher (1959) obtained nodulation in *Ceanothus leucodermis* seedlings by inoculating the soil in experimental containers with small parts of nodules from plants in the field. Von Ploto (1941) successfully infected *Alnus glutinosa* with *Actinomyces alni* isolated from *Alnus incana*. Other investigators have obtained nodule formation in plant roots by inoculation with the ground up nodules or material isolated from the nodules of other plants of the same and different species (Schaefer 1943). If the nitrogen fixing role of bitterbrush root nodules can be completely verified, this technique might be extended to include field inoculation of areas having plants without nodules. Direct application of nitrogen would also probably improve the soil, but the effect would not be as permanent as with a symbiotic organism.
2. Insufficient sulfur had a limiting effect on the growth of lettuce indicator plants and seemed to limit root growth in *P. tridentata* in the pumice soil. The loose, coarse, porous texture of this soil indicates that water and nutrient availability could be closely related to the extent of the root system. The addition of sulfur might increase the density and survival of bitterbrush plants by its favorable effect on their roots.
3. The fact that nodules were not found on plants grown in the pumice soil may have been due to the absence of the causative organism. How-

ever, it is also possible that a toxic factor in the soil inhibited the growth of nodules on these plants, or that this soil environment is in some other way unsuited to perpetuating the nodule-causing agent even though it should be introduced. The effect of sulfur or some other deficiency or a combination of the two may also be important factors to consider in obtaining nodulation.

SUMMARY

The nutrient status of 2 soils in which bitterbrush plants occur naturally was determined by pot tests using Romaine lettuce, *Purshia tridentata*, and *Purshia glandulosa* plants as nutrient indicators.

In one soil, a reddish brown loam formed on basaltic rock, phosphorus deficiency limited shoot but not root growth of the indicator plants. Root growth was not significantly limited in this soil by other nutrients (N, K, S) tested.

In the second soil, a coarse-textured pumice, both shoot and root growth of indicator plants were limited by an indicated nitrogen deficiency. Sulfur deficiency seemed to limit the root growth of *P. tridentata* plants.

Bitterbrush plants grown in the basalt soil appeared to have a source of nitrogen that was not available to the lettuce plants grown in the same soil. Nodules were present in the roots of all of the bitterbrush plants grown on this soil. The nodules in the roots of the bitterbrush plants grown in the basalt soil contained a symbiotic organism that may have had the ability to fix atmospheric nitrogen.

Both bitterbrush and lettuce plants showed limited growth in the pumice soil with a —N +PKS treatment. Nodules were not present in the roots of any of the bitterbrush plants in this soil.

These tests provide valuable clues to the nutrient status of the soils studied and could be used to study problems of bitterbrush growth, density and distribution.

One possibility for improving the nutrient status of bitterbrush soils is to inoculate the roots of individual plants or large soil areas with the nodule-causing organism. This could increase the available nitrogen in soils which previously contained the organism by increasing the number of nodules in any individual plants. In soils which lacked the symbiont, the inception of nodules should be even more favorable on bitterbrush plant growth unless inherent soil factors precluded their establishment.

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VEGETATION CHANGE INDUCED BY ELEPHANTS AND FIRE IN MURCHISON FALLS NATIONAL PARK, UGANDA

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Spectacular changes from arboreal to grassland vegetation in Murchison Falls National Park are obvious to the most casual observer, as indicated by: isolated dead trees, straggling survivors, groves of dead trees, logs in treeless grassland, root sprouts of former savanna trees, survival of fire-resistant species, debilitation of forests, and the presence of forest-grown trees in open grassland. In the present paper evidence for these changes is presented together with hypotheses as to the causes of the vegetational changes and the probable future vegetation under prevailing conditions.

The Park encompasses 3,900 km² of relatively flat land 2° north of the equator in Uganda, East Africa (Fig. 1). Elevation averages 800 m from a low of 625 m along the Albert Nile River. Rabongo Hill (1,303 m) stands out as a monadnock in the eastern portion of the Park, and Igisi Hill (1,286 m) forms another conspicuous landmark south of the park. Rainfall varies from 100 to 125 cm annually and falls mostly in thunderstorms during the "long rains" from April through June and the "short rains" in September and October. Despite pleasantly uniform temperatures from 20°C at night to 30°C at midday, the

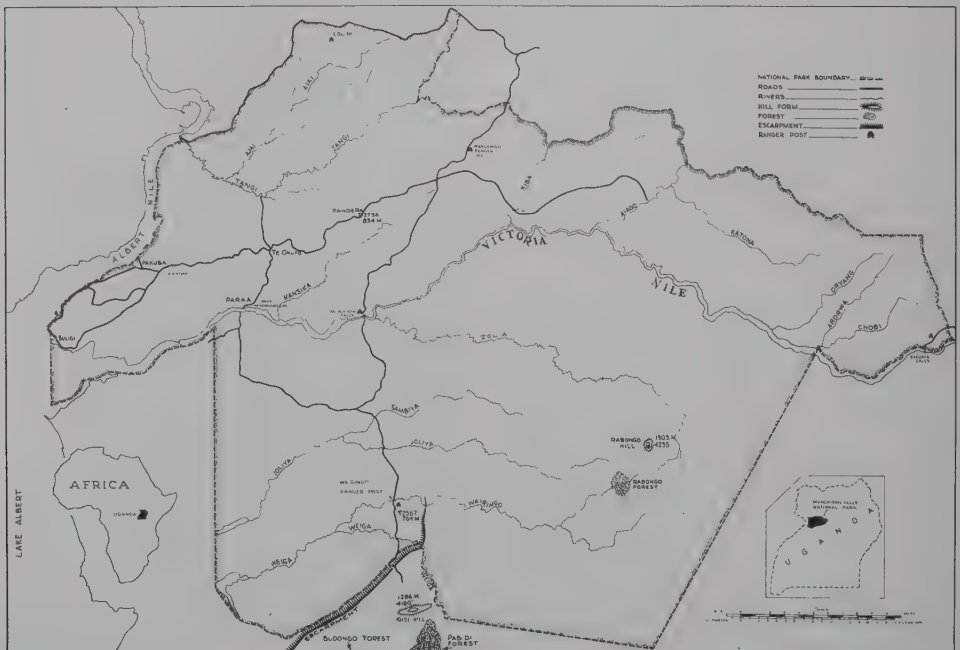


FIG. 1. Map of Murchison Falls National Park. The southern boundary is 2° north of the equator.

climate enervates human beings. Temperatures at midday may reach 35 to 40°C during the dry season in January and February.

As soon as the grassy vegetation is combustible in late December, fires are set by local people until the whole countryside is burned over within a period of three weeks. This practice predates the presence of white man. Some fires spread over 200 km²; few are larger and many are smaller in area. No attempt is made to control fires, except around dwellings. The basic purpose of burning seems to be to provide grassy vegetation for wild and domestic ungulates and to make new growth available. But ease of hunting through increased visibility and maneuverability, driving wild animals with fire, and burning for the pleasure of seeing a fire also contribute to the annual practice of burning.

The vegetation of the region is shown by Phillips (1959) as "More Luxuriant Subhumid Wooded Savanna" with some "Humid Forest with Derived Savanna; *in situ* Forest Relics Frequent." Shantz and Marbut (1923) designate the vegetation as "High Grass-Low Tree Savanna." This type of vegetation occupies most of Uganda and forms an almost continuous border around the tropical rainforest of the Republic of the Congo.

About three-fourths of the vegetation in the Park presently consists of fire-induced grassland. The next largest physiognomic type includes sparsely wooded to thickly wooded grassland, the latter achieving its best development in the north-eastern portion of the Park, north of the Victoria Nile River. Groves of palm (*Borassus aethiopum*) occur along the major streams. Riparian or gallery forests are found in strips along streams, as circular patches in moist sites around springs, and in oblong patterns where the land is swampy during the rainy seasons. Two small woodlands occur in the Park, one at Wairingo Ranger Post and the other at Pandera. High tropical rainforest is represented by one remnant near Rabongo Hill.

All types of woody vegetation are in the process of conversion to grassland under the combined influence of elephants (*Loxodonta africana*) and fire. Large trees are killed by fire damage to tissues exposed by the action of the animals in gouging, peeling, and ripping the bark while foraging and rubbing on the boles of the trees. Over most of the area south of the Victoria Nile conversion to treeless grassland has been completed. Without protection from fire, the continued existence of woodland is impossible as the

canopies are opened more and more with the death of trees debarked by elephants and subsequently damaged by fire. Because of intense concentrations of elephants seeking shade, small relicts of gallery forests are vanishing. The disappearance of high forest is much slower, but no less certain, than other kinds of arboreal vegetation.

VEGETATION IN THE PAST

Documentary evidence

That the vegetation immediately south of the Victoria Nile was predominantly grassland in 1864 is evident from the observation of Baker (1866: 158) at Shooa Morū between Karuma Falls and Murchison Falls: "the whole country was a wilderness of rank grass that hemmed us in on all sides. . . ." The note was made from a high point 3 km south of the river.

Describing the vegetation between Fort Magungo near the mouth of the Victoria Nile and Kiróto (Fort Kikoroto) 10 km east of Igisi Hill, Schweinfurth *et al.* (1888: 18-21) report: "The whole stretch of country is covered by grass, so that horse and rider, much more wanderers on foot, are entirely hidden in it. Scattered throughout this sea of grass are Leguminosae, ten to fourteen feet high, with yellow blossoms, tree-like Solanae, tall thistles, single trees (*Kigelia*, *Mimosa*, *Combretas*, and a few *euphorbias*), and in some places the tall spikes of an aloe, covered with hundreds of beautiful red tubular blossoms spotted yellow. The monotony of the way is often broken by a banana plantation . . . and now and then one comes upon a hut, or group of huts. . . . In all directions well-worn paths across the country, a testimony to the intercourse of the natives among themselves. The last part of the road to Kiróto is rendered almost impassable by the luxurious and entangled growth of grass. . . . A ceaseless monotony envelops the traveller upon these marches, grass and isolated trees, and reeds of gigantic dimensions, often forming regular walls on either side. Sharp and prickly *Cyperus* and *Vassia* grass intermingle with *randia* and *mimosas*. Quite unexpectedly one gets a sudden blow from some hidden tree-stump, or tear from some prickly thorn, of which the most destructive are thistles, six feet high, with large leaves, snow-white on their underside, and round white or purple heads. . . ."

The first detailed map of the region was prepared in 1905 by Vandeleur (1897: 472). The area east of the Albert Nile, south of the Tangi

River, and west of Te Okuto is shown as "wooded." Southward, between Buligi and Paraa, the area is designated as "open grass plain." An area half way between Igisi Hill and the Victoria Nile in the vicinity of the present-day Wairingo Ranger Post is described as "wooded." The approximate position of the Rabongo Forest is also shown as wooded. Immediately southeast of Murchison Falls and in two locations between Igisi Hill and Masindi, 32 km southward, "grass" is indicated. About 20 villages are shown scattered along the Victoria Nile and the route from Murchison Falls to Masindi.

A sketch map made by Owen (1905) a decade later showed "forest" northwest of the confluence of the Weiga and Wairingo Rivers and "scrub" eastward from the so-called forest. Nothing is

shown in the vicinity of Rabongo Hill. Along the Titi River southeast of the Park the region is designated as "cultivated." If the map is reliable, it indicates that the Wairingo woodland extended considerably farther west than at the present time.

Evidence from relict trees

The impression of treeless grassland given by early explorers seems to be implied from descriptions based on open savannas without adequate reference to the scattered trees. Relict trees provide mute evidence of former vegetation (Figs. 2 and 3). Standing dead trees are sufficiently dense in some areas to indicate the extent of former heavily wooded grassland and woodland. This is the case in the vicinity of Wairingo Ranger Post, between the Weiga River and the Escarpment, northeast of Igisi Hill between the Weiga and Wairingo Rivers, and along the Victoria Nile north of Rabongo Hill. Isolated mature living individuals of *Vitex doniana*, *Terminalia glaucescens*, *Combretum binderanum*, *Combretum guezii*, *Ficus* sp., *Kigelia aethiopica*, and *Azalia africana* remain in broad expanses of open grassland, and standing dead trees of these species were as frequently, if not more frequently, encountered as living specimens in 1958. In areas of grassland where neither living nor dead trees remain standing, fallen trees were often found consumed to varying degrees by repeated fires.

Considerable stretches of country in the vicinity of Rabongo Hill retain isolated forest-grown trees (Fig. 3), dead or dying as a result of repeated burning, but still revealing their forest youth in the growth-form of their boles. The two *Chlorophora excelsa* trees, each estimated on the basis of size to be 100 to 150 yrs old, shown in Figure



FIG. 2. At the edge of the Wairingo woodland dead *Terminalia glaucescens* trees indicate the former extent of the woodland and *Lonchocarpus laxiflorus* is emerging as the only species capable of surviving the effects of annual fires.



FIG. 3. Large trees of *Chlorophora excelsa* stand in open grassland. Coppice shoots of *Markhamia platycalyx*, *Spathodea campanulata*, and *Phyllanthus discoideus* still persisted in the vicinity.



FIG. 4. Understory shrubs, including *Rinorea ilicifolia*, *Argemuellera macrophylla*, *Acanthus pubescens*, and *Lindacheria mildbraedii*, are exposed along the forest edge after the death of large forest trees.

3, had girths of about 4 m. Estimating a growth rate of 1 m in girth every 25 to 50 yrs, a scar about 25 cm deep on one tree indicated that the effect of fire was present 30 to 50 yrs ago. The clean boles indicated that these fire-sensitive trees grew up under forest, or at least dense bush, conditions. The forest itself probably stopped the fire 50 yrs ago. Had the trees grown up under the influence of frequent fires, knarls and scars from small branches would have characterized the growth-form. Associated with *C. excelsa* trees were root coppice of *Spathodea campanulata*, *Phyllanthus discoideus*, and *Markhamia platycalyx*, all of which species are thicket or forest trees. The former two are not likely to occur in wooded grasslands, but *P. discoideus* may develop on termite mounds, producing coppice growth form under the influence of fire. The clear boles of *P. discoideus* adjacent to the *C. excelsa* trees indicated development under forest conditions.

Scattered riparian (gallery) relict forests occur around permanent or intermittent springs in this region of the Park. One such relict was dominated by *Khaya grandifoliola*, with some *Blighia welwitschii* and *C. excelsa* contributing to the canopy, and an understory of degenerating remains of *Diospyros abyssinica*, *Trichilia prieuriana*, *P. discoideus*, *M. platycalyx*, and *Canthium* sp. Some depauperate *Acanthus pubescens*, which may have been one of the pioneer colonizers, also occurred. The exposed flank of this forest was ringed by large *K. grandifoliola* trees, all of which showed buttresses enlarged by callus tissue resulting from repeated debarking by elephants. The clear boles above the scar tissue indicated that the trees had developed in a closed forest. There was no evidence of fire affecting these trees. The animals concentrated in and around the edge of this tiny forest to the point that the grasses were too trampled to burn readily and carry fire to the trees.

A few living trees and many standing dead trees provide clear evidence of about 25 former patches of gallery forest southeast of Rabongo Hill. When seen from the air these relicts are conspicuous in the open grassland.

In swampy areas and seasonally wet places stands of dead *Mitragyna stipulosa* were noted in 1958.

Relict trees may be encountered nearly everywhere in the Park today, attesting to a far greater abundance of trees in the recent past. If extensive treeless grassland existed, it probably occurred between the Zolia and Victoria Nile Rivers where Baker made his observation.

PHOTOGRAPHIC EVIDENCE OF VEGETATIONAL CHANGE

In 1932 aerial photographs were taken of a strip about 15 km wide on each side of the Albert Nile as part of a survey of the water resources of the upper Nile conducted by a British company for the Egyptian government. The individual negatives and prints were destroyed in London during World War II, but a mosaic is still available. In 1956 the same region was photographed in connection with a topographic survey. A conspicuous change in vegetation over the past three decades can be shown in the area immediately northwest of Te Okuto (Fig. 1) by comparing the number of trees in different crown-diameter classes in 1932 and 1956 at precise locations. Trees under 9 m in crown diameter were too small to be seen easily on either set of photographs, and the numbers for this class are not highly accurate. But the larger trees provide evidence (Table I) of the striking change that took place in the

TABLE I. Changes in tree crown diameter distribution between 1932 and 1956 in the Te Okuto area based on 10-hectare samples

Plot Sample Number	NUMBER OF TREES BY CROWN DIAMETER DISTRIBUTION (m)						Total >9
	Year	<9	9-12	12-15	15-18	>18	
1.....	1932	25	65	24	7	0	96
	1956	6	4	1	0	0	5
2.....	1932	79	58	26	8	0	92
	1956	48	4	1	0	0	5
3.....	1932	53	12	16	9	8	45
	1956	10	3	3	1	1	8
4.....	1932	116	78	4	0	1	83
	1956	74	104	27	10	3	144
5.....	1932	143	49	0	0	0	49
	1956	46	21	2	0	0	23
6.....	1932	8	25	25	17	8	75
	1956	13	17	5	7	5	34

span of 24 yrs. The first 10-hectare sample showed considerable additional erosion as well as a 95% reduction in trees with crown diameters over 9 m. In samples 2 and 3, the reduction in large trees was 95% and 82%, respectively. Sample 4 was selected from one of the areas of greatest density of trees in 1956. Many small trees and a few large trees existed at this site in 1932. Maturation of small trees to a relatively dense stand of trees 9 to 12 m in crown diameter is indicated by comparing the two sets of photographs. The same generalization holds for

TABLE II. Large trees composing *Terminalia glaucescens* woodland at Wairingo Ranger Post, based on 10 one-tenth-hectare plots

Species	Plot Number	No. of Trees	LIVING			STANDING DEAD		FALLEN
			Mean size (cm DBH) ^a	Girdling (%) ^b	Vigor Class ^c	No. of Trees	Size (cm DBH)	No. of Trees
<i>Combretum guinezi</i>	8	2	43(40-45)	35(1)	4	0	—	0
<i>Ficus dicranostyla</i>	1	2	75(60-90)	0	1	0	—	0
<i>Ficus</i> sp.....	7	1	90	75	2	0	—	0
<i>Stereospermum kunthianum</i>	7	0	—	—	—	0	—	1
<i>Terminalia glaucescens</i>	1	2	40(30-50)	10- 40(2)	3	0	—	0
	2	5	35(30-55)	50- 90(2)	3	2	25, 25	1
	3	5	35(30-45)	10- 50(2)	3	0	—	4
	4	2	55(45-60)	35-100(2)	5	0	—	0
	5	5	40(30-50)	65-100(5)	5	0	—	0
	6	3	50(35-65)	65-100(3)	4	1	35	0
	7	6	45(35-50)	35-100(6)	4	2	25, 70	3
	8	9	40(30-45)	35-100(9)	4	1	35	3
	9	6	45(35-65)	0	2	2	10, 25	0
	10	5	45(40-50)	35- 90(3)	3	0	—	1

^a Range indicated in parenthesis; DBH=Diameter Breast Height.^b Number of trees indicated in parenthesis.^c Vigor Class from high to low=1 through 5.

sample 5, but the contrast is not so extreme. In sample 6 a 55% reduction in large trees occurred over the 24-yr period.

The area compared in the photographs was designated as wooded on Vandeleur's map. Probably the vegetation in 1895 was thickly wooded grassland, if not actually woodland, and the change in vegetation in this area is perhaps more striking than in most of the Park. Nevertheless, comparable reductions of large trees seem to have occurred in sparsely wooded grasslands, as indicated by relict trees, stumps, and logs.

PATTERNS OF VEGETATIONAL CHANGE

Woodlands to grassland

Terminalia woodland at Wairingo.—In late February, 1958, an east-west line of one-tenth hectare plots (20 by 50 m) was established approximately 500 m south of the Survey Marker (elevation 764 m) at Wairingo Ranger Post. Starting at the main Park road, plots were located at random along the line with a distance of 200 to 300 m between plots. Within the plots, data concerning each large tree were recorded, including diameter at breast height (dbh), vigor, per cent of girth girdled, height of destruction to bark, notes on old and fresh scars, healing of scars, effect of fire on open scars, condition of crown with particular reference to portions living and dead, and other relevant facts. Also, within these same plots the number of stems of trees living geophytically (as root sprouts annually curtailed by fire) was recorded. Pertinent data are presented in Tables II and III. Herbaceous vegetation was examined in 3 one-tenth-meter plots (20 by 50

cm) within each of the large plots, one being located at each end and one in the middle of the one-tenth-hectare plot. Using a modified Hult-Sernander Scale, coverage of vegetation, soil, and litter were estimated as: less than 1% and 1/16 of the plot (Class 1), from 1/16 to 1/8 (Class 2), from 1/8 to 1/4 (Class 3), from 1/4 to 1/2 (Class 4), from 1/2 to 3/4 (Class 5), and from 3/4 to 4/4 (Class 6). Next, the living vegetation was considered as a whole and the amount of coverage by different kinds of plants was estimated, using the same classes. This technique is a modification from Daubenmire (1959); and further details, particularly with respect to the use of a point-analyzer to obtain accuracy and precision, have been reported (Buechner 1960: 120-121).

The nomenclature of trees is according to Eggleling (1952) as revised by Ivan R. Dale and amendment lists issued by the Uganda Forest Department, and the nomenclature of grasses is according to Eggleling (1947a).

It is evident from Table II that *Terminalia glaucescens* was the most abundant large tree in the transect studied. *Combretum guinezi* was not uncommon, and within the same woodland a small stand of *Prosopis africana* was located about 1 km northeast from the transect. Not a single tree of any species was found without scars resulting from gouging by the tusks of elephant. Occasionally a *T. glaucescens* tree was found with the bark completely intact, but in all such cases several completely healed old scars were more or less conspicuous. Altogether the 48 living *T. glaucescens* trees examined contained at least 75 completely closed old scars. Evidently the trees

TABLE III. Trees living geophytically^a

Species	WOODLAND		GRASSLAND ^b	
	<i>Terminalia</i>	<i>Terminalia-Prosopis</i>	<i>Terminalia</i>	Wooded
<i>Acacia hockii</i>	6 (60) ^c	8 (60)	6 (40)	6 (20)
<i>Azela africana</i>	1 (10)	0	0	0
<i>Albizia coriaria</i>	22 (80)	7 (40)	3 (20)	0
<i>Albizia zygia</i>	8 (30)	15 (40)	51 (100)	30 (80)
<i>Annona chrysophylla</i>	0	9 (60)	0	2 (20)
<i>Bridelia schleroneuroides</i>	8 (40)	38 (90)	43 (100)	12 (80)
<i>Combretum binderanum</i>	9 (20)	430 (100)	326 (100)	89 (100)
<i>Combretum guineense</i>	13 (40)	67 (90)	255 (100)	69 (80)
<i>Crataeva adansonii</i>	1 (10)	0	0	0
<i>Dombeya rotundifolia</i>	1 (10)	0	0	0
<i>Ficus</i> sp.....	0	7 (20)	0	0
<i>Gardenia jovic-tonantis</i>	3 (30)	9 (60)	0	6 (80)
<i>Grewia mollis</i>	21 (90)	105 (100)	28 (80)	9 (60)
<i>Gymnosporia senegalensis</i> var. <i>spinosa</i>	0	7 (50)	0	0
<i>Harrisonia abyssinica</i> ^d	97 (80)	10 (20)	62 (80)	30 (80)
<i>Hymenocardia acida</i>	1 (10)	31 (70)	40 (100)	5 (80)
<i>Lonchocarpus laziflorus</i>	222 (100)	69 (100)	132 (100)	163 (100)
<i>Ptilostigma thonningii</i>	1 (10)	9 (30)	0	2 (20)
<i>Prosopis africana</i>	3 (10)	3 (20)	1 (20)	0
<i>Pseudocedrela kotschyii</i>	1 (10)	11 (30)	0	0
<i>Pterocarpus abyssinicus</i>	1 (10)	0	0	0
<i>Securidaca abyssinicus</i>	4 (30)	0	19 (60)	207 (100)
<i>Securidaca viroscd</i>	1 (10)	2 (20)	17 (100)	5 (40)
<i>Stereospermum kunthianum</i>	172 (80)	13 (60)	70 (80)	63 (100)
<i>Strychnos inocua</i>	17 (60)	1,300 (100) ^e	81 (100)	11 (40)
<i>Terminalia glaucescens</i>	314 (100)	220 (100)	362 (100)	34 (80)
<i>Vitex doniana</i>	2 (10)	0	1 (20)	4 (20)

^a Based on 10 one-tenth-hectare plots in each of the woodland sites and 5 one-tenth-hectare plots in each of the grassland sites, the locations of which were: Woodland—*Terminalia glaucescens*, Wairingo Ranger Post; *Terminalia glaucescens*—*Prosopis africana*, Pandera. Grassland—*Terminalia glaucescens* conversion, 1 km north of Wairingo Ranger Post; Wooded Grassland conversion, 9-11 km northeast of Wairingo Ranger Post.

^b Grassland conversions from former *Terminalia glaucescens* woodland and former Wooded Grassland.

^c Number of individuals with frequency in percentage within parentheses.

^d Shrubs living almost entirely in clumps on termite mounds.

^e Based partly on estimates.

have been under attack for several decades. Old scars that had partially healed numbered 25, and fresh scars numbered 20 for the 48 trees. The fresh scars varied from occasional single gouges, caused by the action of one or more strokes of an elephant's tusk, to large rectangular patches from which the bark had been removed completely over an area 30 by 60 cm or greater in measurement. Frequently bark was stripped from 1 to 3 m above the ground, and occasionally to a height of 5 m (Fig. 5). The most severely damaged trees appeared to be ones for which elephants had developed a predilection. Once removal of the bark was sufficiently advanced, the animals repeatedly sought out the same tree rather than attack less-damaged adjacent trees. Gradually the removal of bark advanced around the tree until girdling was complete. The tenacity of life in *T. glaucescens* was amazing. Individuals could be found in all stages of vigor, from a few remaining vigorous trees without open scars to trees in various stages of debility. Some individuals 50 to 60 cm in dbh were recovering so well from repeated

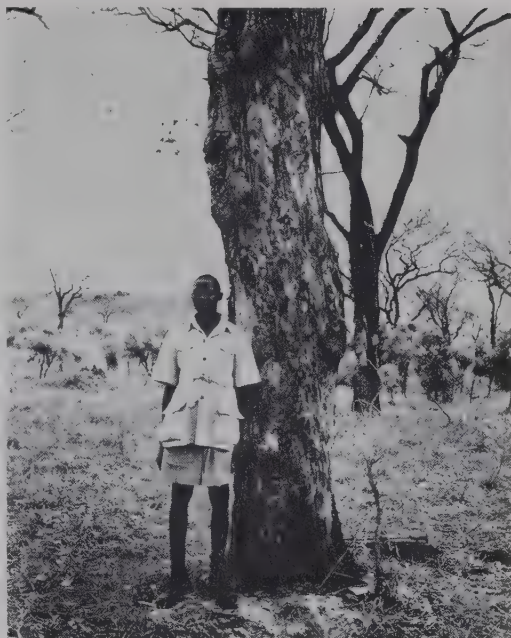


FIG. 5. Elephants removed the bark to a height of 4 m on this *Terminalia glaucescens* at Wairingo Ranger Post.

scarring that, seemingly, they would continue to live for a long time. One tree exhibited remarkably high vigor despite almost complete girdling except for an extremely narrow strip of connecting bark. Seven completely girdled trees retained life, but death of various portions of the crowns indicated that these individuals probably would not live more than another year or two. Once a tree was girdled over 50% of the girth, there seemed little prospect of survival. Some trees with bark stripped from only 10% to 20% of the girth were in a debilitated condition, suggesting that factors other than removal of bark affected longevity. Probably the degree to which burning affected the exposed tissues accounted for much of the variation in time and cause of death between individual trees. From the present condition of *T. glaucescens*, it is evident that under current conditions of annual burning the woodland at Wairingo (Fig. 2) will change drastically within another decade or two.

The future vegetation in this area depends on the ability of species of trees now living geophytically to survive in the *T. glaucescens* woodland (Table III). The 21 species of trees recorded in the transect provide evidence of the former composition of the Wairingo woodland and the surrounding wooded grassland. The most important of these, suggested by the extant wooded

TABLE IV. Large trees composing *Terminalia glaucescens*-*Prosopis africana* woodland at Pandera, based on 10 one-tenth hectare plots

Species	Plot Number	No. of Trees	LIVING			STANDING DEAD		FALLEN
			Mean size (cm DBH)	Girdling (%)	Vigor Class	No. of Trees	Size (cm DBH)	No. of Trees
<i>Ficus</i> sp.....	8	1	75	75	2	0	—	0
<i>Grewia mollis</i>	6	0	—	—	—	2	13	0
<i>Prosopis africana</i>	1	3	30(25-35)	35-30(2)	4	2	15, 30	0
	2	4	30(25-35)	25-50(2)	3	1	35	0
	3	2	35(30-45)	1- 5(2)	2	1	8	1
	4	2	50(45-55)	1(2)	1	2	30, 35	0
	5	5	35(30-40)	25-50(2)	3	0	—	0
	6	2	35(20-50)	10-35(2)	4	0	—	1
	7	3	35(30-40)	50-75(2)	5	1	20	0
	8	0	—	—	—	4	15, 15, 20, 25	0
	9	0	—	—	—	1	20	1
	10	0	—	—	—	2	35, 40	0
<i>Terminalia glaucescens</i>	1	5	35(25-40)	0	1	0	—	0
	2	7	30(25-40)	0	1	2	25, 25	0
	3	1	40	0	1	0	—	0
	5	6	30(25-35)	0	1	2	10	0
	6	1	45	0	2	1	8	0
	7	4	30(25-35)	100(1)	2	1	15	1
	8	1	25	0	2	1	20	1
	9	3	50(40-60)	75(1)	3	0	—	0
	10	1	50	0	1	0	—	0

grassland immediately south of the Park, probably were: *Acacia hockii*, *Albizia coriaria*, *Albizia zygia*, *Bridelia scleroneuroides*, *Combretum binderanum*, *Combretum gueinzii*, *Ficus* spp. *Grewia mollis*, *Hymenocardia acida*, *Lonchocarpus laxiflorus*, *Piliostigma thonningii*, *Stereospermum kunthianum*, *Strychnos innocua*, *Terminalia glaucescens*, and *Vitex doniana*.

In the Wairingo woodland, only *L. laxiflorus* (Fig. 2) seems to be escaping mortal injury from annual burning to which it and all other species are subjected. Currently, dense stands of this species are developing in large openings created through death of *T. glaucescens* trees. Within 6 of the 10 plots, 27 individuals of *L. laxiflorus* were from 2 to 15 cm in diameter, most of them being in the lower range. As shown in Table III, no less than 222 individuals were found living geophytically in the 10 plots, none of which was located in a large opening of the woodland.

Two other species of savanna trees with exceptionally high resistance to fire occurred in the Park woodlands. One of these, *Stereospermum kunthianum*, was present in 80% of the plots at Wairingo. Although 172 sprouts were enumerated, none of them showed evidence of resisting the annual burn sufficiently to achieve aborescent growth. The third species, *Pseudocedrela kotschyi*, was so rare in the Wairingo woodland that it is unlikely to constitute a significant part of the future vegetation. Both species of *Combretum* are also considerably resistant to fire, but neither

species achieved growth beyond the geophytic stage in the Wairingo area. On top of the escarpment immediately south of the Park boundary, about 5 km from the southern flank of the main Wairingo woodland, *Combretum binderanum* was equally as important as *L. laxiflorus* in the composition of dense fire-induced stands of trees reaching a height of 3 to 5 m.

In the Wairingo *T. glaucescens* woodland, and over nearly all of the land in the Park south of the Victoria Nile, *L. laxiflorus* is outstanding among the three most fire-resistant species in successful establishment of coppice growth over large areas.

Herbaceous vegetation, consisting almost entirely of grasses, carpeted the ground in the woodlands. Data on frequency and coverage-when-present were obtained from late February to early April to relate the coverage of grasses primarily to basal area and obtain an estimate of the large amount of exposed bare soil between the grasses. Fires occurred from late December through January, and sufficient regrowth for the purpose of this study had occurred by mid-February. At this time vegetation covered about 10% of the ground, litter about 5%, and bare soil about 85%. In three months of growth the grasses achieved a height of 1-1.5 m, and vertical projection of green material covered nearly 100% of the ground. At Wairingo the important grasses were *Hyparrhenia filipendula*, constituting 50-75% of the living plants in 40% of the plots; *Brachiaria*

brizantha, constituting 25-50% in half of the plots; *Hyparrhenia dissoluta*, forming 50-75% of the grasses where it occurred in 25% of the plots. *Andropogon canaliculatus* with nearly 25% coverage in one-fourth of the plots, and *Panicum maximum* constituting 50-75% of the vegetation where it occurred in the shadiest locations. *Sporobolus pyramidalis* made up 50-75% of the grasses in 10% of the plots. Most of the graminaceous vegetation of the Wairingo area was composed of *H. filipendula* and *B. brizantha*.

Terminalia-Prosopis woodland at Pandera.—Ten one-tenth-hectare plots were established more or less at random in the woodland immediately south of the Pandera Survey Marker (elevation 834 meters), and the same kinds of data were recorded as at the Wairingo woodland 30 km southward (Tables III and IV).

At the time of the investigation in March and April, 1958, the Pandera woodland was characterized by approximately equal numbers of *Terminalia glaucescens* and *Prosopis africana* and a greater amount of *Combretum gueinzii* than at Wairingo (Fig. 5). The composition was changing rapidly in favor of *T. glaucescens* in part because elephants preferred the bark of *P. africana*. The active change is borne out in Table IV. Of

crown of green foliage showed no indication of stress. This example again illustrates the predilection of elephants for revisiting certain individual trees. Within the 10 plots, 16 standing dead *P. africana* trees were counted as against 7 standing dead *T. glaucescens* trees, further substantiating the change toward a woodland dominated by *T. glaucescens*. Destruction of the bark of *P. africana* appeared to be primarily responsible for the high mortality rate, but some nearly dead individuals appeared to be untouched by the animals. Two trees, each about 40 cm dbh and in the lowest vigor class, were sloughing bark from the upper branches as well as the main bole, yet girdling seemed inconsequential. One large *T. glaucescens* (60 cm dbh) with three completely healed old scars and no fresh damage to the bark also was dying from causes other than debarking. Perhaps *P. africana* has a shorter longevity than *T. glaucescens*, in which case the combined effect of mortality factors associated with old age and the preference of elephants for *P. africana* may account for the shift in population toward *T. glaucescens*. Furthermore, *P. africana* may be more sensitive to fire than *T. glaucescens*. Only three sprouts of the former species were located within the plots, compared with 220 of the latter, suggesting a great difference in resistance to fire, although factors other than fire cannot be discounted. It should be noted that the vigor of *T. glaucescens* trees at Pandera was excellent compared with trees of the same species at Wairingo (cf. Tables II and IV). Evidently the species will persist much longer at Pandera than at Wairingo, thus perpetuating the Pandera woodland over a longer period of time. But with the disappearance of *P. africana* the *T. glaucescens* trees may be killed through increased attack by elephants.

Composition of the tree species living geophytically in the Pandera woodland was nearly identical with that of the Wairingo woodland (Table III). There was sharp contrast, however, in the abundance of the various species. At Pandera, *Combretum binderanum*, *Grewia mollis*, and *Strychnos innocua* were far more abundant, and *Lonchocarpus laxiflorus* and *Stereospermum kunthianum* far less abundant than at Wairingo. In the Pandera woodland large openings had not yet resulted from mortality of large trees, and it would be difficult to predict the composition of the future fire-resistant arboreal vegetation. Patches of *L. laxiflorus* were not present in conspicuous stands as at Wairingo, but this does not preclude the possibility of this species becoming the dominant tree in the future. The deep



FIG. 6. *Terminalia glaucescens-Prosopis africana* woodland at Pandera, showing debilitated *P. africana* in the foreground. Dead trees of both species can be seen in the background.

21 trees of *P. africana*, 10 were severely girdled. The vigor class of nearly all individuals was distinctly less than that of *T. glaucescens* trees. Only two of the 29 trees of *T. glaucescens* were girdled, although in these cases 75% to 100% of the girth had been stripped of bark, compared with 25% to 50% for most of the *P. africana* trees. One of the *T. glaucescens* trees had been girdled completely and severely rubbed so recently that the

Kaiso soils and the possibility of slightly more rainfall at Pandera may result in future woody vegetation considerably different from that south of the Victoria Nile. Immediately north of the abrupt discontinuity between the Pandera woodland and the fire-induced grassland, *Pseudocedrela kotschyi* has become established in dense, low coppice over a large area, and it is likely that this species will become important in the vegetation that replaces the woodland.

The graminaceous vegetation in the Pandera woodland was similar to that in the Wairingo woodland, with the exception that *Hyparrhenia filipendula*, *Brachiaria brizantha*, and *Andropogon canaliculatus* were present in greater frequency and formed a more uniform mixture.

High forests near Rabongo Hill

At the headwaters of the Wairingo River, immediately southwest of Rabongo Hill (Fig. 1), seven patches of high closed forest, designated collectively as the Rabongo Forest, covered a total area of approximately 280 ha in 1958. Two large contiguous stands formed about 80% of the complex, and the remaining remnants were isolated in close proximity. These stands appear to be the only survivors of a much more extensive series that once covered the upper Wairingo valley within the past century. Approximately 30 km southwestward, the Budongo Forest of about 43,500 ha has its northeastern limit, while the small Pabidi Forest is situated between the two and almost continuous with the Budongo (Fig. 1). The Rabongo Forest bears affinities in species composition to both the Budongo and the forests of the Acholi District about 100 km northward. The similarity in canopy composition between the Budongo and Rabongo forests indicates that the latter may represent a relict of a former more extensive forest of the Budongo type, although the absence of hygrophytic Marantaceae and Zingiberaceae suggests some kinship also between the more arid Rabongo and the most advanced stage of the Acholi type. With the Budongo (Eggeling 1947b) the Rabongo Forest shows a canopy dominance by *Cynometra alexandri* with *Rinorea* in the understory, together with numerous other characteristic associates. With the west Acholi communities (Dawkins 1949) the Rabongo lacks a hygrophytic ground layer and has *Phyllanthus* and *Sapium* as main colonizers in place of the Budongo's *Maesopsis*, and it also has *Khaya grandifoliola* in place of the Budongo's *K. anthotheca*. When the whole chain of forests from the Semliki valley (about 25 km northwest of Fort Portal, Uganda) to the Imatong

Mountains in the Sudan (Jackson 1956) is considered, there is little doubt that the Rabongo is a relict linking formerly forested areas of west Acholi with the Budongo. They are part of a steady cline from true tropical rainforest to a moist-deciduous high forest, all stages of which can still be found. Without the influence of elephants, the Rabongo Forest probably would represent the most advanced development of the Budongo type. In the "Ironwood Forest Climax" of the Budongo described by Eggeling (1947b: 37-38, 59-60), *Cynometra alexandri* forms over 75% of the canopy and the number of associated tree species is less than half the number found in seral communities. Single-dominant forests of *C. alexandri* occur also in the eastern Congo, across the border from Uganda, north and northwest of the Ruwenzori Mountains (Lebrun 1936).

The species composition of the Rabongo Forest which follows includes at least 80% of the tree species, but the list of shrubs is probably far from complete. Symbols following the plant name indicate abundance in four classes: A = abundant; F = frequent; O = occasional; and R = rare.

Trees of the canopy, commonly 30 to 50 m high: *Aningeria altissima* (O), *Celtis zenkeri* (R), *Cola gigantea* (A), *Chlorophora excelsa* (F), *Chrysophyllum albidum* (F), *Cynometra alexandri* (A), *Entandrophragma cylindricum* (R), *Erythrophloeum guineense* (O), *Ficus mucosa* (R), *Ficus* spp. (epiphytic) (A), *Holoptelea grandis* (F), *Khaya grandifoliola* (F), *Mildbraediodendron excelsum* (F), *Pterygota mildbraedii* (A), and *Schrebera arborea* (F). Trees of the ill-defined understory, 15 to 25 m high, or forming a canopy in immature forest and gaps: *Albizia zygia* (R), *Blighia* sp. (probably *welwitschii*) (O), *Bosqueia phoberos* (F), *Caloncoba schweinfurthii* (F), *Celtis durandii* (O), *Diospyros abyssinica* (A), *Dombeya mukole* (O), *Majidea fosteri* (O), *Markhamia platycalyx* (O), *Melanodiscus* sp. (O), *Phyllanthus discoides* (O), *Premna angolensis* (F), *Pseudospondias microcarpa* (R), *Sapium ellipticum* (O), *Spathodea campanulata* (R), *Strychnos mitis* (R), *Tapura fischeri* (O), *Tetrapleura tetraptera* (O), *Treculia africana* (R), *Trichilia prieuriana* (O), and *Trichilia splendida* (R). Small trees and large shrubs of the lower understory 5 to 10 m in height: *Canthium crassum* (R), *Coffea canephora* (possibly *Belonophora glomerata*) (F), *Craibia brownii* (R), *Conopharyngia holstii* (O), *Euphorbia teke* (R), *Lindackeria mildbraedii* (R), *Monodora* sp.

("gibsonii") (R), *Neoboutonia* sp. (R), *Oxyanthus unilocularis* (O), *Randia urcelliformis* (A), *Rinorea ardisiaeflora* (A), *Ritchiea duchesnei* (O), *Vanqueria acuminata* (F), *Voacanga obtusa* (R), and *Xylopia parviflora* (R). Shrubs from 1 to 3 m high, either in lowest layer of forest or at forest edge: *Acanthus pubescens* (F), *Adhatoda engleriana* (F), *Argomuelleria macrophylla* (A), *Erythroxylum emarginatum* (R), *Rinorea ilicifolia* (A), *Rinorea poggei* (A), and *Securinega virosa* (F).

A transect of 25 point-samples, using the angle-count method (Grösenbaugh 1952) with a basal-area factor of 20 and with 100 m between samples, was established through the largest stand of the Rabongo Forest to obtain more precise information on species composition, population density, and basal area of trees in categories one and two above. Small trees and shrubs of the understory were recorded also, and these data provided the basis for designation of the abundance classes. The basal area above buttress for all canopy trees combined was 19.3m² per ha, of which *Cynometra alexandri* formed 73%. Under natural development probably this species ultimately would dominate the Budongo Forest, most of which presently is a mahogany seral stage (Eggeling 1947b: 37-38). Assuming this interpretation to be correct, the Rabongo Forest is older than most of the Budongo Forest and represents an example of ultimate development of the latter. Therefore, the Rabongo Forest is a unique and important relict not represented by any other forests in the Park or its vicinity. Partially because of the natural physiognomy, and largely as a result of trampling of the vegetation and compaction of the soil by elephants, the Rabongo Forest is unlike most closed high forest in tropical Africa in that it is free from impenetrable thickets of lianas, thorny shrubs, and small trees. Thus, wide shady vistas reminiscent of temperate deciduous woodland provide an unusual character to these forests.

Field research in the Rabongo Forest was conducted in late February, 1958, after the surrounding grasslands had been burned. At this time, snags, stumps, and fallen trees were still burning at the edges of all of the forests and occasionally deep within the smaller forests. Under these conditions, the attrition of the forests from the combined action of elephants and fire could be observed in action. Nearly every tree was damaged to some degree by elephants, but debarking alone rarely caused mortality. Bark scraping and peeling probably would kill few trees in the absence of fire. Severe damage, ultimately resulting in mortality, is caused when fire follows fresh de-

barking before fire-resistant cork layers can be formed. Along the edges of the forests, elephants consumed and trampled understory trees and shrubs such as *Acanthus pubescens*, *Randia urcelliformis*, *Rinorea ardisiaeflora*, *Rinorea ilicifolia*, and *Caloncoba schweinfurthii*. Large trees along the forest edges, including *Chlorophora excelsa*, *Cynometra alexandri*, and *Pterygota mildbraedii*, were being killed by the combined action of debarking and burning. As a result of the destruction of both large trees and the understory along the margins of the forests, light penetration increased sufficiently to permit the spread of grasses, notably *Panicum maximum*, into the forest. Sufficient inflammable material is produced to carry the fire from surrounding grasslands ever deeper into the forests. As a result of debarking, the exposure of dry rotten wood on the boles of trees deep within the forests created a fire hazard. Trees were found smoldering in many locations throughout the smaller forests. In one area degenerating *Khaya grandifoliola*, *Pterygota mildbraedii*, *Holoptelea grandis*, and *Caloncoba schweinfurthii*, once part of the closed high forest, were found entirely surrounded by grassland. Destruction of this part of the forest was so recent that remnants of understory trees and shrubs were found entirely exposed outside the forest (Fig. 4). By these processes along the forest edge and in the heart of small forests, scores of hectares of high forest have been lost within the past decade and many within the past 30 to 40 years.

The possibility of high forest vegetation dominated by *Holoptelea grandis* was seen in the small patches of forest immediately south and southeast of the largest forest. In these small forests, *Cynometra alexandri* and *Pterygota mildbraedii* were dying out, providing suitable conditions for reproduction of the light-demanding *H. grandis*. Although young trees of the latter species were browsed heavily by elephants, no damage occurred to trees after the foliage had escaped the reach of the animals. The bark of *H. grandis* has a strong iodine odor and taste, which may account for the animals' failure to attack the bark of this species. A few fully mature individuals of *H. grandis*, which is one of the canopy components throughout the central African tropical rainforests, were observed in the Rabongo Forest. Vigorous stands of trees 15 to 60 cm in diameter above the buttress were observed in one of the smaller forests—indicating the type of forests that may develop under continued influence by elephants, provided fire is controlled. Unless protected from excessive debarking and fire, the *Cynometra alexandri* forests at Rabongo may

become superseded by *H. grandis* and its cohort, *Schrebera arborea*.

Elephant-induced forest communities dominated by *H. grandis* occur in the West Nile District of Uganda, the most well-developed being the Bula Forest (160-ha) on the Ora River about 16 km east of Okollo (Eggeling 1935). Few tree species other than *H. grandis* are found in these forests, which are characterized by scant understorey vegetation, much exposed ground, and greatly compacted soils.

Increase of Lonchocarpus laxiflorus vegetation.

The development of *Lonchocarpus laxiflorus* vegetation under the influence of annual burning was illustrated well in a transect of 10 plots at Te Okuto. The community at this location differed from much of the *L. laxiflorus* vegetation developing elsewhere in the Park by the presence of a palm component, *Borassus aethiopum*. Excellent groves of mature palm trees occur along the lower Tangi River (Fig. 1). Elephants appear to be fond of the ripened fruit, and in making their way upslope toward Te Okuto the animals distribute the seed in fecal droppings. The *L. laxiflorus*-*B. aethiopum* vegetation extended almost continuously from the Tangi groves of palm up the gentle slope to the Pandera woodland and represented one of the most notable examples of increased density of arboreal vegetation in the Park. Both *L. laxiflorus* and *B. aethiopum* occurred in each of the 10 random plots. The latter ranged from 3 to 55 individuals in a single plot, with a total of 257 for the 10 plots. None of these individuals achieved tree growth-form, probably because fire prevented development beyond the incipient leafy stage. *L. laxiflorus* trees were distributed in dbh classes as follows: 2-5 cm, 105; 5-8 cm, 76; 10-13 cm, 34; 13-15 cm, 6; 15-18 cm, 5; 18-20 cm, 2. The average number per hectare was 326 individuals. *Crataeva adansonii* occurred in half of the plots for a total of 11 individuals and one *Acacia sieberiana* tree was found in each of two plots. Based on 30 one-tenth-meter plots, about 15% of the ground was covered by vegetation, 80% by bare soil, and 5% by litter. Of the green herbaceous vegetation, *Hyparrhenia filipendula* formed about 75%; *Brachiaria brizantha* about 15%; and the remaining 10% was distributed, in order of importance, among *Brachiaria kotschyana*, *Hyparrhenia dissoluta*, *Panicum maximum*, *Andropogon canaliculatus*, *Chloris gayana*, and several forbs.

As the fire-sensitive components of the original vegetation gradually become eliminated, *L. laxiflorus* remains as the predominant tree species

and spreads over wide areas. Its importance in the vegetation of the Park, especially south of the Victoria Nile, will increase with time. The grassland physiognomy of the vegetation is at present disrupted by extensive patches of *L. laxiflorus* which appear destined to expand, particularly on sites of better soils and suitable moisture. Probably it will increase both as a scattered component of open grassland and as nearly pure stands of small woodland. Large expanses of dense low coppice already present provide ample evidence of the trend toward development of open *L. laxiflorus* woodlands. Currently, these trees seldom exceed 3 m in height, but strong resistance to fire and rapid growth are evident. It may be anticipated that growth will reach 15 m and that *L. laxiflorus* will become the most important tree species in the Park.

POSSIBLE TREND IN VEGETATION CHANGE

Within the converted grasslands sufficient root coppice of at least 30 species of savanna trees remains to provide for the reestablishment of former wooded grassland and woodland under control of fire (Fig. 7). Mean annual rainfall is 100 to 125 cm for this region, according to the map published in 1959 by the Lands and Surveys Department of Uganda, and limited records from stations within the Park show rainfall to be in the upper part of this range. Rainfall of such magnitude is sufficient to support heavily wooded grassland, woodland, and forest. It is through the combined influence of fire and elephants that much of the vegetation in the Park south of the Victoria Nile is now primarily treeless grassland. Under continued annual burning, the species of trees incapable of surviving geophytically ultimately will vanish, leaving fire-resistant *Lonchocarpus laxiflorus*, *Pseudocedrela kotschyi*, *Stereospermum kunthianum*, *Combretum binderanum*, *Combretum gueinzii*, and *Combretum molle* as potential components of future vegetation. So far, it appears that *L. laxiflorus* is the most successful of these species in escaping serious injury from the annual fires, and this species seems to be gaining importance as a scattered element in nearly pure grassland and as a dominant in wooded grasslands. Some patches are so dense that seemingly they will develop into closed woodland. *P. kotschyi* covers considerable area between Pandera and Wangkwar Ranger Post, and also around Lolim, but south of the Victoria Nile it was observed only as an occasional individual and never in significant stands. The future of fire-resistant species of trees depends upon the time of burning. Early burns in late December



FIG. 7. This view of derived grassland in the vicinity of Rabongo Hill shows root coppice of about 30 species of trees exposed after the grasses were burned. The *Clorophora excelsa* trees of Figure 3 are in the center.

and early January tend to promote establishment of these species, whereas deliberate late burning results in fires so hot that few trees of any species survive.

DISCUSSION AND RECOMMENDATIONS

Although no early data are available as a basis for accurate assessment of the increase in numbers of elephants during the past half century, it seems likely that a remarkable increase has occurred. Upon release from organized hunts required for protection of scattered settlements, the animals increased greatly in the present Park area after removal of the entire human population about 1912 (Eggeling 1947: 33-34). The Budongo Forest alone was thought to be the headquarters of an estimated 5,000 elephants more than 35 years ago (Swynnerton 1924). The population of elephants increased within the Park area not only as a result of natural increase of resident individuals, but also as a result of immigration and concentration as harassment increased in

regions to which the animals migrated. Two of the main migrations routes have been eliminated completely. Increased agriculture, accompanied by control of crop-raiders through shooting, along the principal remaining migratory route has encouraged concentration within the Park and vicinity. As the amount of land man is willing to set aside for elephants in central Uganda continues to decrease, the Park and surrounding area will become more and more overpopulated by these animals. It is already evident that an overpopulation is developing and that control of numbers will be necessary in the near future to prevent severe destruction to the vegetation and degradation of the entire habitat. In fact, to avoid the grave consequences of an overpopulation, a carefully controlled program of regulating numbers should begin immediately. The number of elephants involved has been established through 12 complete aerial counts over a study area of about 4,000 km² which includes all of the Park south of the Victoria Nile and the immediate

vicinity surrounding the Park. The lowest count was 4,141 individuals and the highest was 12,389 (Buechner, et al. 1961), migration accounting primarily for the vast difference in numbers. The mean population is about 7,000 to 8,000 animals.

An increase in numbers of elephants appears to be the only change in the ecosystem that could have been responsible for setting into motion the profound changes in vegetation that have occurred and continue to take place. By removal of bark in foraging and rubbing activities elephants expose functional tissues to fatal damage by fire, causing death of the large trees and expansion of grassy vegetation. As more flammable grass material became available the destructive force of fire, with respect to trees, increased in intensity and spread over a wider area. The role of elephants probably shifted in the process of vegetation change from an initial triggering action, in the presence of fire, to one of accelerating the change, finally becoming nonessential in the perpetuation of grasslands. In contrast, fire increased in importance as the vegetation changed, and currently it is an essential factor in the maintenance of grassland vegetation.

Next to man, elephants are probably the most adaptable animal in ability to occupy a wide variety of habitats and utilize an extremely wide range of food. Prior to the conversion of savanna, woodland, and forest vegetation to grassland in the Park, these animals may have foraged on a varied diet of many species of trees and grasses, whereas presently they are being restricted more and more to a diet of grasses. Grasses may be the preferred diet even in the presence of abundant browse, according to Buss (1961). Conceivably, elephants could subsist entirely on grasses. But that will not become necessary in the Park because of the abundance of *Lonchocarpus laxiflorus*. The foliage and stems of this species are utilized so readily that unbrowsed individuals are seldom found, yet the heavy foraging does not prevent rapid growth and spread by coppicing. Irrespective of whether a varied diet is essential to elephants, it is clear that some browse is desired when available. Perhaps this explains the difference in greater amount of damage to trees in the Wairingo woodland compared to the Pandera woodland. The former is smaller in area (about 1,500 ha) and is surrounded by open grassland, whereas the latter is approximately three times larger and located north of the Victoria Nile where wooded grassland vegetation is far more extensive. Access to an abundant supply and great variety of browse

north of the river may alleviate the need, or desire, for feeding on the bark of trees. Although the density of the animals in the Park north of the river appears to be somewhat less than south of the river, the concentration within the woodlands, at least during certain times of the year, appears to be such that destruction of trees cannot be attributed to a difference in number of elephants. Possibly the tremendous reduction of browse south of the Victoria Nile, where elephants have increased most and the conversion to grassland has been most complete, may be one reason why debarking is more severe on trees in the *Terminalia glaucescens* woodland at Wairingo than in the Pandera woodland. Selection of bark as food is seasonal in the case of the deciduous *T. glaucescens*, which is leafless during the dry season from early January to early March, and feeding on bark is concentrated during the period of regrowth of the foliage when the bark will peel. Possibly the taste of the rising sap satisfies the elephant's palate, or perhaps the bark and sap contribute important nutrients to the diet. Whatever the reason, elephants debark *T. glaucescens* trees to the extent that, combined with burning, the habit contributes to mortality of the trees.

In view of the extraordinary changes taking place in vegetation, it is essential to define clearly the objectives of nature conservation in the Park. Two basic approaches are required. First, consideration must be given to surveillance over individual species of plants and animals from the point of view of preserving endemic flora and fauna, these terms being used in the sense of kinds of plants and animals without reference to their abundances. Decisions must be made as to the species to be preserved, including introduction of animals not endemic to the area. Second, consideration must be given to surveillance over populations and communities of plants and animals from the point of view of preserving vegetation and animal life. It is as vital to preserve communities of *Terminalia* woodland and *Cynometra* forests as it is to preserve a population of elephants if a national park is to be developed in the broadest sense for conservation of nature.

The most urgent problem is to halt attrition of the Rabongo Forest, not only because it is the only example of high forest in the Park, but also because it represents a distinct type of mature tropical rainforest found in the eastern Congo and western Uganda. Already these forests have been modified by the influence of elephants especially in the small patches. However, through prevention of fire by patrolling firebreaks during the brief fire season, the Rabongo Forest could be

perpetuated for a few more decades. In the smaller forests the canopy has been disrupted sufficiently to permit reproduction of light-demanding *Holoptelea grandis*, favored in survival by freedom from debarking by elephant. Thus with control of fire, elephants may continue to modify the vegetation to produce high (40 m) forests dominated by *H. grandis*. While it may be possible to control fire and preserve a sample of high forest, it seems impracticable to control the animals sufficiently to perpetuate a forest dominated by *Cynometra alexandri*, as the Rabongo Forest consists of small islands in the midst of an open grassland and is extremely attractive to elephants. Although modified from its natural form, the Rabongo Forest would continue to be of great scientific value.

Equally as important, in terms of preserving vegetation, are the *Terminalia* woodlands. Although it may be too late to save the Wairingo woodland, there is considerable hope for perpetuating, by control of fire, the woodland and its associated animal life in the Pandera portion of the Park.

Unless measures are taken to conserve forest, woodland, and other types of vegetation in the Park, loss of endemic species of plants and animals and natural communities will be considerable and scientific and recreational values will deteriorate.

SUMMARY

In Murchison Falls National Park, located in tropical Uganda, East Africa, luxuriant wooded grasslands, *Terminalia* woodlands, *Cynometra* rainforests, and riparian forests are in the process of conversion to treeless grassland through the combined action of elephants and fire.

Comparison of aerial photographs taken in 1932 and 1956 showed 55-59% reduction in trees with crown diameters greater than 9 m in four 10-hectare samples and an increase in large trees resulting from maturation of small trees in two other samples.

In a *Terminalia* woodland, 48 living and 8 dead *Terminalia glaucescens* were examined in 10 one-tenth-hectare plots. None of the living trees was free from scars resulting from debarking by elephants, and nearly all were in a low state of vigor. In a *Terminalia-Prosopis* woodland 10 of 21 trees of *Prosopis africana* were severely girdled and 16 trees of this species were found dead in 10 plots, whereas only 2 out of 29 trees of *T. glaucescens* were girdled sufficiently to cause death within another year.

Except for *Lonchocarpus laxiflorus*, root sprouts of 27 species of trees are unable to achieve

tree growth because of annual destruction of the shoots by fire. As the woodlands and the scattered trees in grasslands are destroyed, grassland vegetation characterized by *Hyparrhenia filipendula*, *Brachiaria brizantha*, and *Andropogon canaliculatus* increases in distribution.

An isolated forest dominated by *Cynometra alexandri* decreased greatly in area over the past four decades to about 280 ha by 1958 as a result of invasion of fire along the forest edge. Consumption and trampling of understory trees and shrubs by elephants combined with mortality to large trees resulting from debarking and burning permitted sufficient light penetration for the spread of *Panicum maximum* and other grasses into the forest margin. As a result, fire from surrounding grasslands is carried ever deeper into the forest, bringing about rapid attrition of the forest vegetation. High forests dominated by *Holoptelia grandis*, the bark of which is free from attack, may develop if the forest margins are protected from fire.

The basic cause of these conspicuous, rapid changes in vegetation seems to lie in an extraordinary increase in the population of elephants resulting from (a) evacuation of people from the area in 1912 because of sleeping sickness and (b) concentration of elephants in the sanctuary because of harassment in regions to which the animals formerly migrated in large numbers. While the animals may have initiated the change, their action is no longer essential in perpetuating the trend toward grassland vegetation.

Under present conditions 30 to 40 fire-resistant species of trees are unable to attain maturity. These species continue to live geophytically, and they impart a conspicuous ragged appearance to the vegetation when exposed from tall *Hyparrhenia* grasses after burning. Sufficient coppice reproduction of all species of trees is present to provide for regrowth of mature woody vegetation in the absence of fire. The most fire-resistant species of trees include *Lonchocarpus laxiflorus*, *Pseudocedrela kotschyi*, and *Stereospermum kunthianum*, but only the first species has resisted burning sufficiently to form a significant component of grasslands and develop new communities of arboreal vegetation.

Nature conservation within a national park should embody preservation of natural vegetation as well as animal life, and to accomplish this objective, in Murchison Falls National Park two policies are essential: (1) The regulation of numbers of elephants to prevent overpopulation and consequent destruction to vegetation and habitat.

(2) The perpetuation of representative examples of past vegetation by control of fire.

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SEASONAL VARIATIONS OF THE PHOTOSYNTHETIC EFFICIENCY AND CHLOROPHYLL CONTENT OF EPIPHYTIC MOSSES¹

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INTRODUCTION

For the past 10 years statistical analyses and physio-ecological studies of the community of epiphytic mosses on forest trees have been carried out in our laboratory. Previous analyses indicated that the ecological distribution of epiphytic mosses is the principal reason for the gradients of light and water on forest trees.

Hosokawa and Odani (1957) measured the daily compensation period (DCP) of some dom-

inant corticolous mosses on beech trees and demonstrated the correlation between the DCP values and the vertical distribution on the trees of those species. Hosokawa and Kubota (1957) pointed out that osmotic values of corticolous mosses tend to increase gradually upward along the trunk from the ground level to the topmost-branches. Odani (unpublished) measured experimentally the photosynthetic rate of epiphytic mosses under varying light intensities and relative humidities. These studies indicated that the upper limit of the vertical distribution of these mosses on forest trees is restricted primarily by water and the lower limit by light.

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This paper reports (a) seasonal variations of the photosynthetic efficiency of epiphytic mosses on forest trees; (b) patterns of the photosynthetic efficiency of these mosses growing at different heights on the trees; (c) seasonal variations of the chlorophyll content of the mosses; and (d) the spatial distribution in height on trees of the chlorophyll content of epiphytic mosses.

MATERIALS AND METHODS

The field work was carried out on 3 trees of *Carpinus tshonoskii* Maximowicz growing near Itaya Pass of Mt. Seburu about 20 km south-east of Fukuoka City; the trees are on the north slope of 38.4° at about 600 m, where the exposure is N 58.0° E. They are in a forest dominated by *Carpinus tshonoskii* Maximowicz and *Parabenzoil trilobum* Nakai, and are about 13-15 m high and 40-60 cm dbh. The forest floor is covered sparsely with *Hydrangea luteovenosa* Koidzumi and *Struthiopteris amabilis* Tagawa.

Each tree was divided from the ecological standpoint into three major parts: the stump, the trunk and boughs, and the topmost-branches (Fig. 1). To study the dominance and composition of epi-

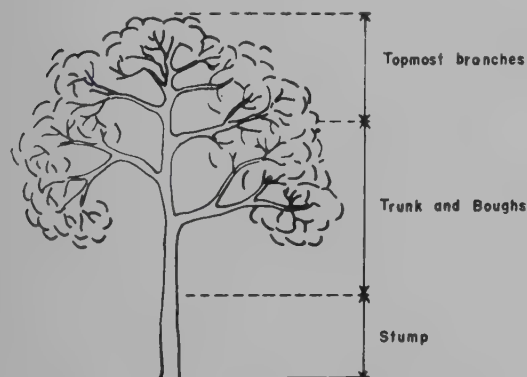


FIG. 1. The provisional division of the forest tree for field experiment and collecting experimental materials: the stump, the trunk and boughs, and the topmost-branches.

phytic mosses on each part, three quadrats were arbitrarily established at different exposures: on the exposed, the sheltered, and the partly sheltered sides. Quadrat sampling indicated that the following mosses predominated at the respective levels:

Stump Species

Thuidium toyamae Nog.
Leucobryum neilgherrense C. Muell.
Hypnum oldhamii (Mitt) Jaeg.
Dolichomitriopsis diversiformis (Mitt) Nog.

Trunk and bough species

Peterobryum arbuscula Mitt.
Neckera konoii Broth.
Macrosporiella scabriseta Dix. et Ther.
Dolichomitriopsis diversiformis (Mitt) Nog.

Topmost-branch species

Ulota crispula Mitt.
Macromitrium gymnostomum Sull. et Lesq.

These mosses were used for laboratory analyses of seasonal variations in photosynthetic rate and chlorophyll content or to correlate the former with the latter. Some additional species including these mosses were also used to analyze the spatial distribution of the chlorophyll content. Micro-environmental factors in each part of the tree, i.e., light intensity, atmospheric relative humidity and air temperature, were also measured (Fig. 2). Light intensity in lux was measured with a Mazda actinophotometer, held vertically on the exposed surface of the trunk. Values from the 3 heights were expressed as a percentage of a similar reading taken outside the forest in full sun at approximately the same time. To compensate for minor fluctuations caused by variation of the amount of cloudiness, recordings were made in triplicate and the mean calculated. The atmospheric relative humidity at the 3 levels was estimated immediately above the moss plants by Assmann's aspiratory psychrometer. Air temperature at stump level was measured by a recording thermometer, while at the two higher levels it was done hourly by maximum and minimum thermometers only during the daytime.

Seasonal variations of the photosynthetic rate and chlorophyll content of epiphytic mosses were estimated at 2-month intervals from April, 1959, to February, 1960. Plants were shaded and watered frequently before measuring to reduce loss of vitality, particularly during the hot summer months. After a thorough soaking in distilled water, plants were blotted dry and any dead parts removed, since the respiration of micro-organisms in these parts appeared to decrease the rate of apparent photosynthesis. Only the green stems and leaves were used for photosynthetic measurements.

The apparatus used in the experiment is a modification of one designed by Boysen-Jensen, made by N. Odani (unpublished). The test materials were placed in an assimilation chamber and illuminated at 800, 2000, 8000, 16,000 and 40,000 lux. Illumination intensity was varied by changing the distance of a 300-Watt reflector lamp, and the temperature was maintained constant ($20 \pm 1^\circ$) by controlling the circulation

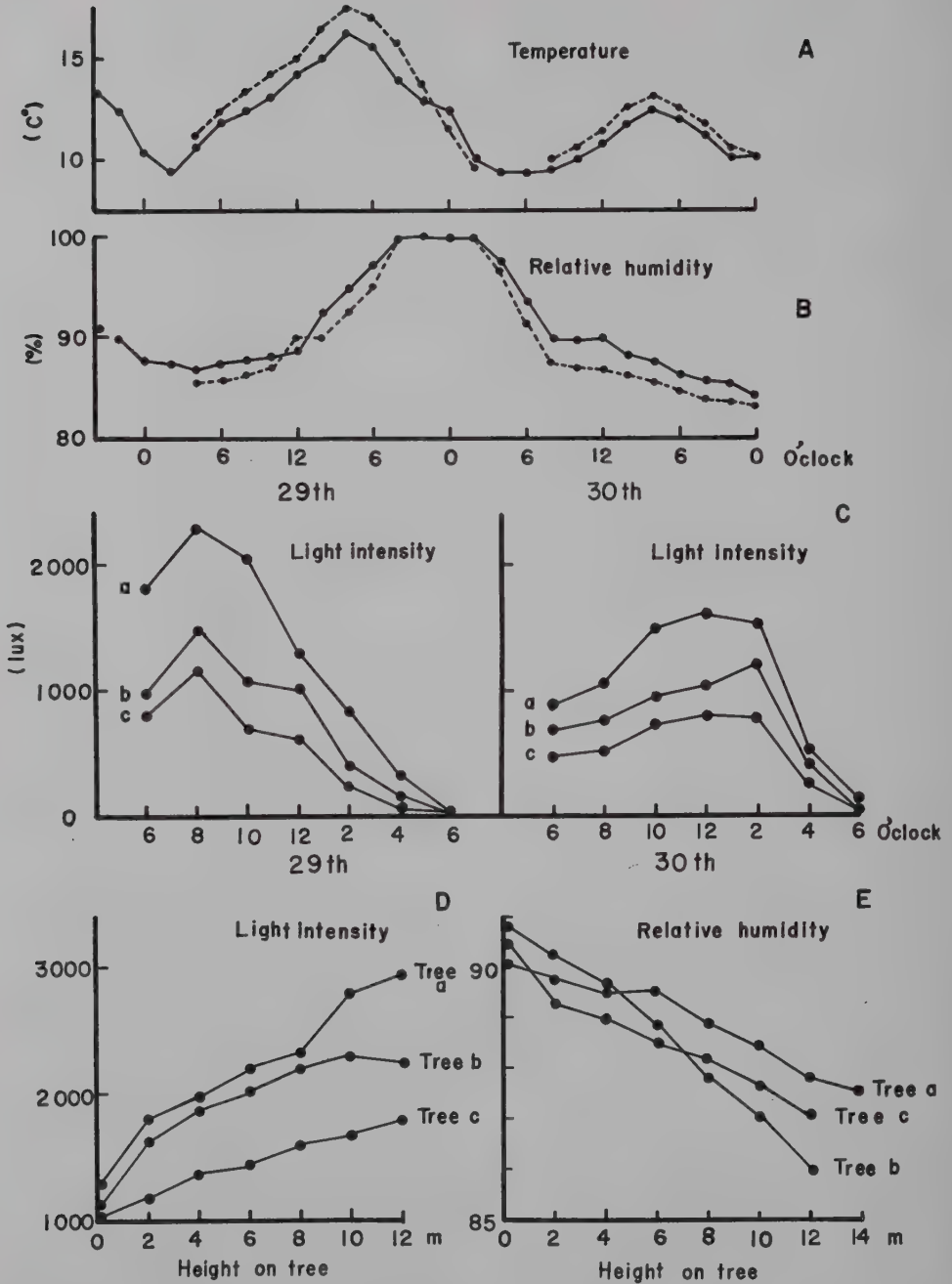


FIG. 2. This shows the result of the field measurements on micro-environmental factors on the tree, October 28-29, 1959. (A) The fluctuation in air-temperature. A recording thermometer was used at the stump level (showing by a solid line). At the trunk and bough level (undescribed) and the crown level (showing by a broken line), measurements were taken hourly during the daytime, but only maximum and minimum values at night. (B) The fluctuation of the atmospheric relative humidity. Relative humidity was measured

of cold water in a bath in which the assimilation chamber was placed. Considerable care was taken to avoid mutual shading of the moss shoots and to maintain 100% relative humidity in the chamber by passing the air through a humidity regulator. Since most mosses are poikilohydric, their gaseous exchanges may be influenced greatly by even a slight alteration in atmospheric humidity. The air in chamber was sampled after pre-illumination at each light intensity for 15 mins. The photosynthetic rate was estimated by the CO_2 -uptake rate of a given plant material under the experimental conditions. Subsequently, green stems and leaves were oven-dried at about 50°C for a few days and a determination of the total chlorophyll concentration was made on an Hitachi-spectro-

photometer, measuring the absorption at 645 and 663 $\text{m}\mu$ in acetone extracts, according to the procedure described by Arnon (1949).

RESULTS

Seasonal variations of the photosynthetic efficiency of mosses on the forest tree

Figure 3 expresses graphically the seasonal variations in photosynthetic rate of some dominant species in each part of the tree. Most species showed the maximum photosynthetic rate in late August, but in the two stump species maximum was in late October. The minimum value of the all species was in late April. More fluctuation in the pattern of seasonal variations of a

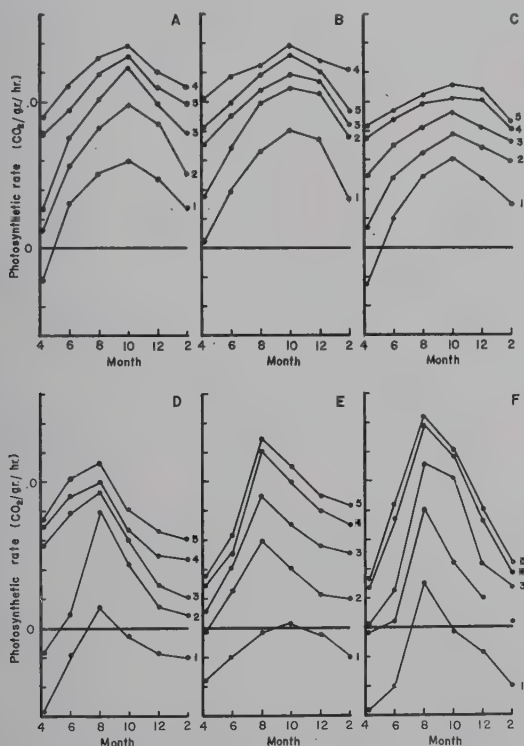


FIG. 3. Seasonal variations of the photosynthetic rate of epiphytic mosses. (A) *Thuidium toyamae*, (B) *Leucobryum neilgherrense*, (C) *Neckera konoii*, (D) *Ulota crispula*, (E) *Macromitrium gymnostomum*, (F) *Pterobryum arbuscula*. Each number in the figure represents the grade of illumination intensity under which the photosynthetic rate of the plant materials was measured: (1) 800 lux, (2) 2000 lux, (3) 8000 lux, (4) 16,000 lux, (5) 40,000 lux.

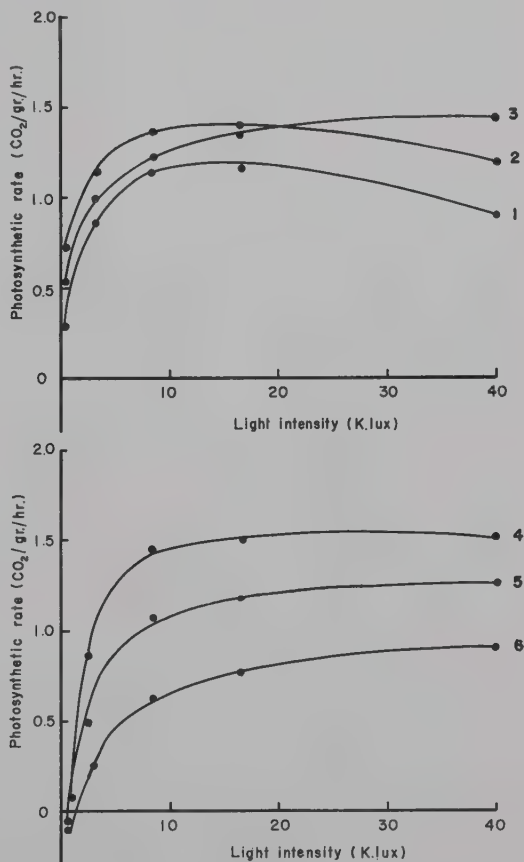


FIG. 4. The photosynthetic curves of epiphytic mosses. (1) *Thuidium toyamae*, (2) *Leucobryum neilgherrense*, (3) *Neckera konoii*, (4) *Pterobryum arbuscula*, (5) *Macromitrium gymnostomum*, (6) *Ulota crispula*.

hourly at the stump level (solid line), throughout the day by an Assmann's aspiratory psychrometer, but at the crown level (broken line) during the daytime. (C) the daily fluctuation of the light intensity on the trees. The measurements of the present factor were carried out at the stump (c), the trunk and boughs (b), and the crown (a) level hourly during the daytime by a Mazda actinophotometer. (D) The vertically gradual changes of the light intensity on the forest trees. (E) The gradual changes of the relative humidity.

given species was obtained at weaker illuminations, but the general patterns resembled each other irrespective of the differences in illumination. In other words, the greater the light intensity the smaller the seasonal fluctuations of the photosynthetic rate. There is no species in a negative CO_2 -balance at 2000 lux or more at any time during the year.

Patterns of the photosynthetic efficiency of mosses growing at different heights on the tree

Results of the influence of light intensity on the photosynthetic rate of epiphytic mosses under conditions of saturated humidity are given in Figure 4. The photosynthetic rate of *Thuidium toyamae* and *Leucobryum neilgherrense*, the stump species, first increases sharply as the light intensity increases. Then gradually, as the light intensity saturation point approaches, it tapers off and finally decreases at the highest intensity.

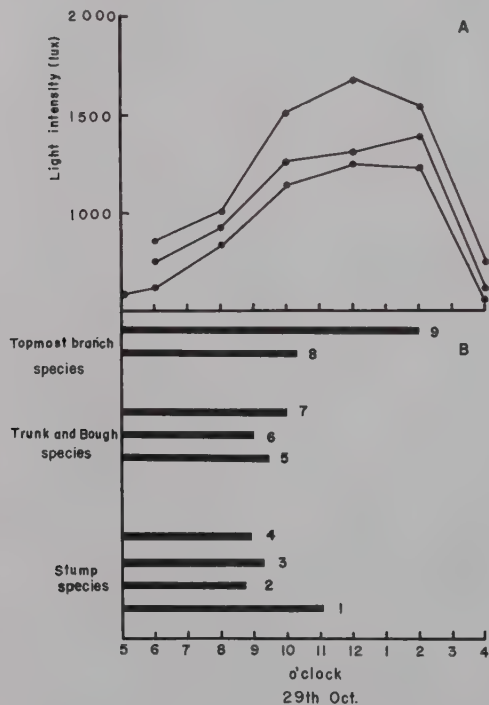


FIG. 5. The daily fluctuation of the light intensity on the tree (A) and the value of the daily compensation period (DCP) of epiphytic mosses (B). (A) Each number represents a different level of height on the tree: (1) stump level, (2) trunk and bough level, (3) topmost-branch level. (B) (1) *Thuidium toyamae*, (2) *Leucobryum neilgherrense*, (3) *Hypnum oldhamii*, (4) *Dolichomitriopsis diversiformis*, (5) *Neckera konoi*, (6) *Pterobryum arbuscula*, (7) *Okamuraea cristata*, (8) *Macromitrium gymnostomum*, (9) *Ulota crispula*.

The photosynthetic rate of *Ulota crispula* and *Macromitrium gymnostomum*, the topmost-branch species, increases rather slowly at first and then steadily with increase of illumination; it increases slightly even at the higher intensities. That of *Pterobryum arbuscula* and *Neckera konoi*, the trunk and bough species, is intermediate between other 2 groups. The compensation point was not measured; however, the light saturation curve indicated that it is below 15,000 lux in all the species.

Figure 5 shows the DCP value on October 29, 1959, of some dominant epiphytic mosses growing at different levels.

Seasonal variations of the chlorophyll content of epiphytic mosses

Figure 6 illustrates the seasonal variations of the total chlorophyll content of epiphytic mosses. In most species, the minimum value was obtained

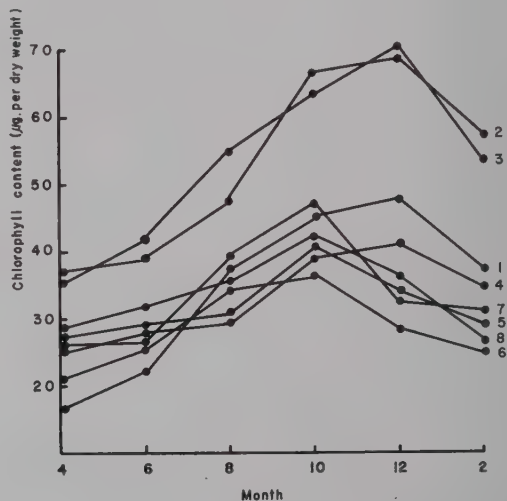


FIG. 6. The seasonal variation curves of the total content of chlorophyll of epiphytic mosses. (1) *Thuidium toyamae*, (2) *Leucobryum neilgherrense*, (3) *Plagiothecium nemorale*, (4) *Macrosporiella scabriseta*, (5) *Neckera konoi*, (6) *Pterobryum arbuscula*, (7) *Ulota crispula*, (8) *Macromitrium gymnostomum*.

in late April and the maximum in October or December. The maximum of the total content of 3 stump species and a trunk and bough species appeared in December, while that of 2 topmost-branch and 2 trunk and bough species was in October. The differences between the minimum and maximum were more conspicuous in the stump species than in the species of the other two. The total content of the stump species, *Thuidium toyamae*, in December was about 3

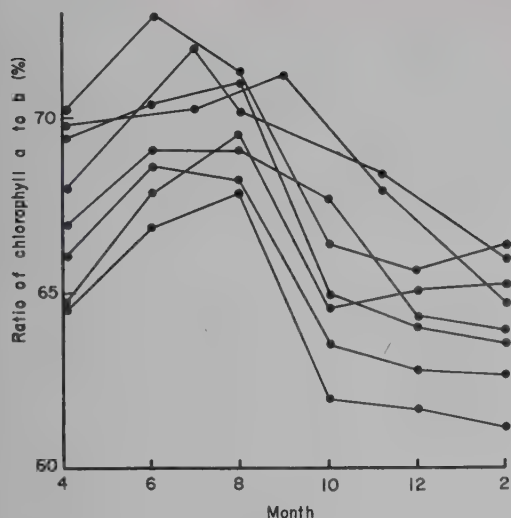


FIG. 7. The seasonal variation curves of the ratio of chlorophyll *a* to *b* of epiphytic mosses. The number in the figure is the same as that in Fig. 6.

times as high as in April and that of *Leucobryum neilgherrense* in December was about twice as high as in April. On the other hand, the total chlorophyll content of most species at higher levels was not more than 1.5 times that of the April value. Most species showed the maximum content in October or December followed by an abrupt decrease in February.

From these data, the ratio of chlorophyll *a* to *b*

was calculated and graphed (Fig. 7). All the species showed similar patterns of variation; i.e., the ratio values, relatively lower in April, increase to the maximum in June or August and then decline gradually.

The height distribution on the tree of the moss chlorophyll content

The dominant and several other moss species were sampled from each of the three trees in August, 1959. The results are in Figure 8. Each value represents the average with its fiducial limit of 3 values of the measurements in a given species. The 4 stump species, except for *Hypnum oldhamii*, seem to have a higher total content of chlorophyll than the 2 groups at higher levels, but the stump species show less difference in total content among the 3 trees than do the higher groups. There are no statistically significant differences in the total content in most instances between the trunk and bough species and the topmost-branch species.

The spatial distribution of the ratio of chlorophyll *a* to *b* was analysed from the data on the total content of chlorophyll (Fig. 9). The ratio of *a* to *b* in the topmost-branch species is slightly higher than that of the other 2 groups, but the differences in the ratio of *a* to *b* between the 2 groups at lower levels is not statistically significant. The differences of the ratio *a* to *b* in the same species among different trees is rather small.

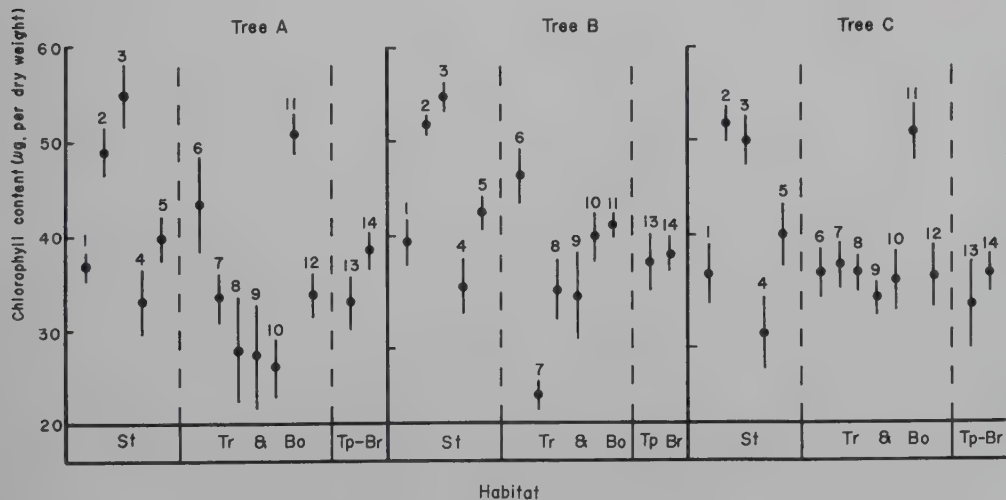


FIG. 8. The spatial distribution (in height on the trees) of chlorophyll content of epiphytic mosses. (1) *Thuidium toyamae*, (2) *Leucobryum neilgherrense*, (3) *Hypnum oldhamii*, (4) *Plagiothecium nemorale*, (5) *Dicranum japonicum*, (6) *Dolichomitriopsis diversiformis*, (7) *Pterobryum arbuscula*, (8) *Neckera konoi*, (9) *Boulaya mittenii*, (10) *Macrosporiella scabriseta*, (11) *Anomodon giraldii*, (12) *Okamuraea cristata*, (13) *Ulotia crispula*, (14) *Macromitrium gymnostomum*.

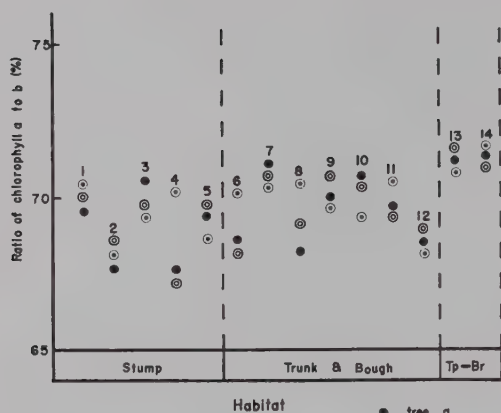


FIG. 9. The spatial distribution (in height on the trees) of the ratio of chlorophyll *a* to *b* of epiphytic mosses. Number in the figure is the same as that in Fig. 8.

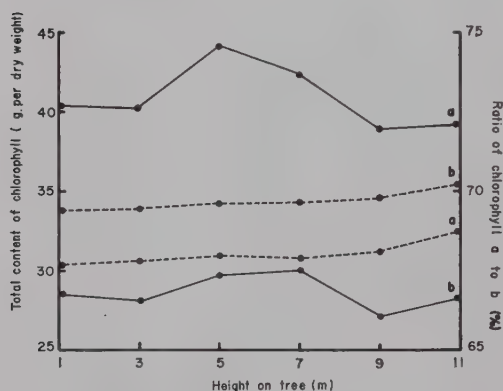


FIG. 10. The spatial distribution curves in height of chlorophyll *a* to *b* of *Dolichomitriopsis diversiformis* (a) and *Macrosporiella scabriseta* (b) growing on different levels of height on a tree. Total content of chlorophyll is shown in a solid line and the ratio of chlorophyll *a* to *b* in a broken line.

Quadrat data suggest that *Dolichomitriopsis diversiformis* and *Macrosporiella scabriseta* have wide amplitudes of tolerance on the tree, though the latter grows at the stump of only one tree of the 3. To investigate the spatial distribution in height of the total content and the ratio of chlorophyll *a* to *b* of these ubiquitous species on one tree, sample materials were taken at 2 m intervals from the ground to the uppermost part of crown. Although a smooth curve could not be obtained in both species from these measurements, the peak of these curves was coincident with the maximum dominance of each species in its vertical distribution (Fig. 10).

DISCUSSION

There is some information for vascular plants of seasonal variations in photosynthetic rate, respiration, transpiration, pigment concentration, osmotic value of cell sap, leaf morphology, anatomy, etc. In lower plants, especially phytoplankton or algae, many detailed studies have been made on the seasonal variation of productivity and pigment concentration but for mosses few reports have been presented.

Bourdeau (1959) measured the CO_2 -exchange of young shoots of several coniferous evergreens shortly after bud opening under certain conditions of light and temperature for one year, and observed that their photosynthetic activity became positive in June and reached its maximum at the end of the growing season. In winter it decreased to almost nothing and increased again the following spring. The chlorophyll content fluctuated throughout the year, the maximum value occurring in late October and the minimum in early June. Bourdeau noted a slight but significant reduction in winter in the photosynthetic rate of the plants kept under uniform conditions throughout the year. Possibly, this was due to an endogenous rhythm of the plants. Clark (1956) followed the CO_2 -uptake of needles of various ages in white spruce and balsam fir from May to October. Little variation occurred within each age-class, except for the new needles. The photosynthetic rate did not become positive before mid-June, while the Norway and blue spruces studied by Bourdeau showed positive in May. Pisek and Winkler (1958) reported the results of a similar investigation.

According to Saeki and Nomoto (1958), the photosynthetic activity of *Zelkova serrata*, a deciduous tree, and the evergreens *Shiia sieboldi*, *Pittosporum tobira* and *Cinnamomum camphora*, increased rapidly in late spring and the higher rates of photosynthesis persisted for about 3 months. The maximum value in most species was attained in late August; afterward the efficiency of the deciduous species decreased gradually until the time of defoliation in November. That of the evergreens fell to a low level in late autumn and continued low throughout the winter. The value of the light compensation point was higher in late spring, decreased abruptly in early summer and then remained constant at the low level until the end of the growing season. The chlorophyll content of *Zelkova serrata* fluctuated in parallel with the photosynthetic rate.

Terrestrial and epiphytic mosses remain green and develop new shoots slowly even during the winter; thus their general pattern of seasonal vari-

ation of the photosynthetic rate and chlorophyll content is similar to that of many vascular plants, especially the evergreens in the temperate zone. Our results seem to support this. The seasonal fluctuation of the photosynthetic rate in epiphytic mosses may result from the seasonal fluctuation of the air temperature rather than from variation in relative humidity and light intensity, unless the general climate varies abnormally during the year. The higher rainfall and denser fog in summer and the lower rate of evaporation in winter in the mountain forest of south-west Japan (Tagawa 1959) would be more favorable to the growth of such poikilohydric plants as mosses.

The fact that the maximum photosynthesis of several epiphytic mosses occurs a few months later than that of evergreens may be due to the suitability of such temperature condition as obtain in early fall. The general trend in seasonal variation of the chlorophyll content is approximately consistent with that of the photosynthetic efficiency; the maximum value in all species occurs in November or December, one or 2 months later than that of the photosynthetic rate. This may mean that the rather abrupt fall of air temperature in early autumn affects the photosynthetic apparatus more strongly than the chlorophyll content. The influence on the photosynthetic rate of defoliation in *Carpinus tshonoskii* in late autumn is not detectable, while the reduction of total chlorophyll content of *Ulota crispula* and *Macromitrium gymnostomum*, both the topmost-branch species, and a few trunk and bough species in December may be due to the defoliation of the trees. It may be difficult for ecologists to elucidate the causality of the seasonal variation of the relation of chlorophyll *a* to *b* in epiphytic mosses.

Measuring the photosynthetic efficiency under given conditions of the light intensity, atmospheric relative humidity and temperature throughout the year may diminish its ecological significance because of such artificial conditions, especially in winter. It is certainly desirable that such measurements should be taken under as natural conditions as possible; perhaps the measurements under the given conditions are valuable in the study of the potentiality (endogenous rhythm) of the photosynthetic rate of epiphytic mosses.

Survey of the micro-environmental factors on beech trees indicates that the light intensity increases gradually along the trunks from the ground to the crown level, and relative humidity decreases conversely (Omura, Nishihara and Hosokawa 1955). Thus it may be expected that the mosses at stump level are sciophytic, those of topmost-branch level are heliophytic, and

those at the middle level are intermediate. The concentration of chlorophyll in sun and shade plants of different species, or in sun and shade individuals of the same species, and its effect on the production of oven-dry matter, were studied by Lubimenko (1908), Kusumoto (1957a, 1957b) and many others. Böhning and Burnside (1956) presented light saturation curves of apparent photosynthesis of 8 sun and 5 shade species. The light saturation and compensation points for the sun species were 2000-25000 ft-c and 100-150 ft-c, respectively. For shade species the light saturation point was recognized at the maximum of 1000 ft-c and some shade species the light saturation intensities were noted as low as 400-500 ft-c.

Because of close photochemical relationships between photosynthesis and chlorophyll pigment, several studies have been attempted from a physiological viewpoint so that the quantity of chlorophyll might be used to measure a magnitude of the photosynthesis. Willstätter and Stoll (1919), Briggs (1922), Gabrielsen (1948) and others have pointed out that the quantity of the chlorophyll is not always related to the amount of photosynthesis except for the linear regression of the photosynthetic curve in weaker intensities of light illumination. It is now believed that the quantity of chlorophyll cannot be a limiting factor for photosynthesis under relatively high light intensities except in species unusually low in chlorophyll.

Randall (1953) studied the chlorophyll content of forest herbs in southern Wisconsin in relation to the vegetational continuum. The continuum was divided into 9 equal intervals and the chlorophyll content of 10 dominant forest herbs was measured in each interval. He described a gradually increasing curve with an average value of chlorophyll content per unit area or per unit weight of dry matter of the leaf of the 10 species from the low continuum value to the higher.

In spite of adopting the different apparatus in this study from Odani's (unpublished), the light assimilation curve of epiphytic mosses accords well with his. The stump, trunk and bough species all maintain positive CO₂-balances below 1000 lux, and all show the seasonal fluctuation in compensation point. The maximum rate of the photosynthetic efficiency is attained at or near 15,000 lux in the stump species, and at or near 25,000 lux in the trunk and bough species. In the topmost-branch species the photosynthetic rate is nearly negligible even at 1000-1500 lux and reaches the light saturation point just at 40,000 lux with increasing the light intensity. The light

saturation point in epiphytic mosses hardly fluctuates seasonally, whereas the absolute value of the photosynthetic rate fluctuates seasonally. Thus, the moss plants growing on the topmost-branches have heliophytic characters, those on the stump sciophytic, and those on the trunk and boughs are intermediate. The DCP values from the field studies are in accord with the above information.

Although the stump species showed more dense concentration of chlorophyll than the groups at higher levels, significant differences in the chlorophyll content cannot be detected among most species of 2 other groups. Accordingly, the vertical changes of the microclimatic conditions on the tree may be so gradual, and there is not recognized any prominent difference in chlorophyll content of the corticolous species growing at different levels on the tree. Smaller fluctuations in the total content of chlorophyll of the same species growing at the stump level among the 3 trees suggest that more stability of the microclimate is expected in the lower part of tree; the moss plants of the upper levels live in the frequently changing microclimatic conditions.

It may be expected that the ratio of chlorophyll *a* to *b* would be higher in hygrophytic plants than in xerophytic plants as a whole. Hosokawa and Kubota (1957) observed that *Ulota crispula* and *Macromitrium gymnostomum* have relatively higher osmotic values and wider ranges of resistances to drier atmospheres. On this basis, therefore, the higher values are probably caused by rather drier atmospheric humidity than higher light intensities in their habitats.

Finally, if detailed studies were carried out in another season, it is quite possible that the spatial distribution of the chlorophyll content in epiphytic mosses would be entirely different.

CONCLUSION AND SUMMARY

This is an investigation of (1) seasonal variations of the photosynthetic efficiency and chlorophyll content of epiphytic mosses on forest trees; (2) the spatial distribution in height of mosses on the trees; and (3) photosynthetic saturation levels of epiphytic mosses at different heights on the trees. Mosses were collected at 2 month intervals from April, 1959 to February, 1960 from *Carpinus tshonoskii* Maximowicz, the dominant forest species near Itaya Pass of Mt. Seburi, Fukuoka, southwest Japan.

Photosynthetic rate was measured by Boysen Jensen's apparatus (modified), and chlorophyll concentration by spectrophotometry.

Generally the seasonal variations of the photosynthetic rate and chlorophyll content of some

dominant epiphytic mosses are similar to those of higher plants, especially the evergreens in the temperate region.

The minimum photosynthetic rate occurred in late April for all of the dominant species on the trees. In most species the maximum value occurred in late August; however, the 2 stump species, *Thuidium toyamae* and *Leucobryum neilgherrense*, showed the maximum in late October.

The minimum content of chlorophyll was observed in late April, while the maximum value of the mosses at lower levels occurred about one or 2 months later as compared with the species at higher levels.

Light saturation curves indicate that the moss plants characteristic of the lower levels have sciophytic characteristics, those of higher levels have heliophytic ones and those at intermediate levels have intermediate ones.

ACKNOWLEDGMENT

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RESPONSES OF *AGROPYRON CRISTATUM*, *A. DESERTORUM*, AND OTHER RANGE GRASSES TO THREE DIFFERENT SITES IN EASTERN NEVADA

RICHARD E. ECKERT, JR.,¹ A. T. BLEAK,¹ JOS. H. ROBERTSON,² AND E. A. NAPHAN³

Concepts of soil-plant relationships developed gradually during the last century and a half. Clements (1928) credited DeLuc, in 1806, with making definite the concept of correlations between plants and soil characteristics. Clements (1928) also believed that Hilgard, in 1906, was the first to formulate fully a concept of plant indicators in soil studies. In 1927, Kittridge recognized the need for a basic correlation between vegetation and soil.

Correlations between vegetation and soil have developed from studies emphasizing soil (Gardner and Retzer 1949, Weislander and Storie 1952), vegetation (Daubenmire 1942, Billings 1945, Tisdale 1947), or a combination of both (Spillsbury and Tisdale 1944, Billings 1949, Poulton 1955, Eckert 1957). All these studies attempted to relate certain soil units (great soil group, soil series, soil type, and/or soil phase) to certain vegetation units (seral plant communities or climax plant association). Two better known vegetation-soil units are Daubenmire's "habitat type" (1952) and the "range site" developed by technicians of the Soil Conservation Service (Dyksterhuis 1951). Similar vegetation-soil units represent biological units of similar environment and therefore of similar productive potential. Although ecological classification research has been in progress for some years, only minor direct use has been made of the results in range-seeding investigations. In striving for greater production from the range resource, it is pertinent to know whether any particular introduced species respond

similarly over a wide variation in environmental factors or whether a species or its varieties responds more favorably in one environment than in another. In other words, to what degree are plant species or varieties sensitive to different sites and how can this knowledge be used to insure greater success in range improvement.

The purpose of this study was to characterize 3 unlike adjacent sites and to describe the responses of several seeded grasses growing under these 3 sets of environmental conditions since 1941.

DESCRIPTION OF THE STUDY AREA

Topography

The study was conducted at the 6000-ft elevation within the Ruby Substation of the Intermountain Forest and Range Experiment Station, 6 miles west of Wells, Nevada (41°5'N, 115°3'W).⁴ The study area included 3 sites: a narrow stream bottom, 3-4% slope (lower site), small alluvial cone peripheral to the stream bottom, 12-14% slope (middle site), and southeast facing slope of 22-24% (upper site). All 3 were within one square acre, itself within a well-grassed 100-acre exclosure (Fig. 1).

Vegetation

All sites originally supported big sagebrush (*Artemisia tridentata* Nutt.). Low sagebrush (*A. nova* A. Nels.) was also present on the upper site. The principal grasses on the lower site were *Elymus cinereus* Scribn. & Merr., *Poa nevadensis* Vasey, *Stipa columbiana* Macoun, and a small amount of *Agropyron trachycaulum* (Link) Malte. On the middle and upper sites, *Oryzopsis hymenoides* (Roem. & Schult.) Ricker,

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³Soil Conservation Service, U. S. Department of Agriculture, Reno, Nevada.

⁴Average annual precipitation at Wells, Nevada, elevation 5628 ft, is 9.36 in.

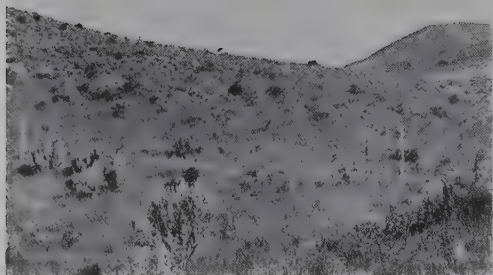


FIG. 1. General view of the study area toward the northwest, 16 years after seeding. White stakes indicate location of transects on the lower, middle, and upper sites.

Sitanion hystrix (Nutt.) J. G. Smith, *Poa secunda* Presl, and *Agropyron spicatum* (Pursh) Scribn. were the principal grasses.

Soil

The soils of the 3 study sites (Fig. 2) were described as follows:⁵

Lower Site—Soil on the lower site is an imperfectly drained Humic Gley developed in medium-textured alluvium derived from granodiorite, gneiss, shale, quartzite, and some basalt and limestone. It is deep, fertile, and moderately permeable and is located on a narrow stream bottom where it is subject to stream overflow and a seasonal high water table in the deeper portion

⁵ Complete morphological descriptions are on file at the State Office of the Soil Conservation Service, Reno, Nevada.

of the soil profile between 36 and 60 in. No injurious salt concentrations occur in any horizon.

Middle Site—Soil on the middle site is a moderately well drained Humic Gley developed in gravelly, moderately coarse textured alluvium derived from the Miocene Humboldt Formation. The Humboldt Formation near this site includes poorly sorted calcareous gravels, sands, silts, and soft shale derived on a small alluvial cone adjacent to the narrow stream-bottom on which the lower site is located. It receives additional moisture from runoff and probably is subject to seasonal high water table in the deep portion of the profile. Injurious quantities of soluble salts are not present in any horizon.

Upper Site—Soil on the upper site is a well-drained Brown Soil developed in calcareous, gravelly, moderately coarse colluvial material derived locally from the Miocene Humboldt Formation. The Humboldt Formation near this site includes poorly sorted calcareous gravels, sands, silt, and soft shale derived from a wide mixture of igneous and sedimentary rock. The soil is located on a hillside. Runoff is medium and little or no additional moisture is contributed from higher areas. Injurious quantities of salt are not present in any horizon.

General features of soils at the sites—Chemical and physical characteristics of these soils are in Table I. Each soil represents a distinct series. These soils have not been correlated; therefore no series names will be used. The soils on the lower and middle sites are similar except for drainage, texture of the subsoil, and parent material. Soil on the upper site has a well developed

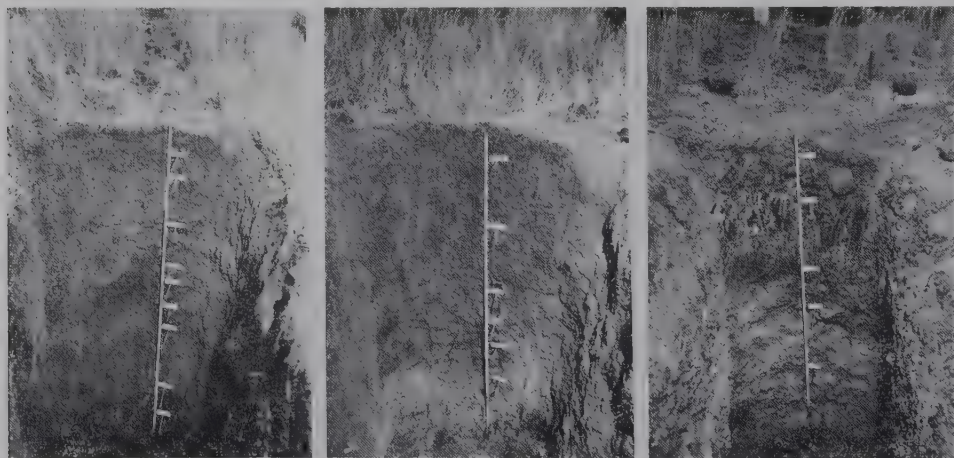


FIG. 2. Soil profiles on the lower (L), middle (C), and upper (R) sites. Photos by Leonard Smith.

TABLE I. Chemical and physical characteristics of the soils from the three sites¹

Site and horizon	Depth (inches)	PARTICLE SIZE DISTRIBUTION (percent) ²				pH ³	Est. (% salt) (Bureau cup) ⁴	Organic matter ⁵	C/N	MOISTURE TENSIONS	
		gravel	sand	silt	clay					$\frac{1}{3}$ atmos. (%) ⁶	15 atmos. (%) ⁷
LOWER											
A ₁₁	0 - 7½	25	41	38	21	7.0	.03	6.89	14.4	25.8	14.0
A ₁₂	7½-17½	17	41	36	23	7.0	.02	4.39	14.4	23.7	11.4
C ₁	17½-30	26	54	26	20	7.2	< .02	2.27	12.1	16.2	9.8
C ₂	30 -35	6	38	41	21	7.3	.03	3.08	13.2	22.4	11.4
A ₁₁ ^b	35 -45½	38	50	30	20	7.4	.02	2.95	12.0	19.4	9.4
A ₁₂ ^{bc}	45½-67	20	35	40	25	7.9	.04	3.48	13.7	28.9	13.5
C ₁ ^b	67 -80	12	37	41	22	7.7	.04	2.01	9.2	28.1	13.2
MIDDLE											
A ₁₁	0 - 5	42	61	23	16	6.9	< .02	4.06	16.8	16.8	8.6
A ₁₂	5 -18	37	59	24	17	7.0	< .02	2.17	11.3	15.5	8.6
A ₁₃	18 -33	58	56	23	21	7.3	< .02	1.65	10.0	15.9	8.7
C ₁	33 -47	36	57	23	20	7.7	.03	1.26	9.0	14.8	8.2
C ₂ ^{ca}	47 -55	38	60	20	20	7.9	.03	.95	9.0	15.9	8.0
C ₃ ^{ca}	55 -74	44	61	20	19	8.3	.02	.69	7.8	15.7	9.2
UPPER											
A ₁	0 - 5	27	46	25	29	7.1	.03	1.84	12.0	17.3	8.6
B ₂₁	5 -14	34	40	14	46	6.7	.05	1.51	10.2	27.9	20.3
B ₂₂	14 -30	43	56	14	30	7.0	.05	.57	8.2	20.2	13.2
B ₃ ^{ca}	30 -42	53	47	32	21	7.6	.03	.34	6.2	13.8	8.7
C ₁ ^{ca}	42 -54	51	74	12	14	8.1	.02	.15	6.0	10.3	5.8
C ₂ ^{ca}	54 -76	60	77	11	12	8.3	.02	.14	4.4	9.8	5.3

¹ Analyses made by Utah State University following Agricultural Handbook No. 60. ² Bouyoucos (1951). ³ Methods 2 and 21a. ⁴ Method 5. ⁵ Method 24. ⁶ Method 30. ⁷ Method 31.

textural B horizon. All have high C/N ratios in the A horizons, indicating that a response could be expected from nitrogen fertilization. All 3 appear to be well supplied with phosphorus. Neither soluble salts nor exchangeable sodium is excessive. The outstanding characteristics of the 3 soils relative to grass production appear to be those associated with moisture relationships.

The soil on the lower site has a deep profile with a low gravel content. This soil is situated on a narrow stream bottom where slope is not conducive to rapid runoff and where additional moisture is supplied by runoff from adjacent slopes. The moisture-holding capacity was estimated to be 12-13 in. for the 80 in. depth sampled.

The soil on the middle site is a deep, gravelly loam with somewhat excessive underdrainage. The available moisture-holding capacity was estimated to be 7-8 in. for the 74 in. depth sampled.

The soil on the upper site is so situated that more runoff can be expected than from the middle and lower sites. Infiltration characteristics, as interpreted from soil morphology, are not as good as for the other 2 soils. Increases in conductivity, exchangeable-sodium, and exchangeable-sodium percentage at the 42-76 in. depth indicate that moisture from normal precipitation rarely wets and passes completely through the profile. Avail-

able moisture-holding capacity was estimated to be 6-7 in. for the 76 in. depth sampled.

METHODS

The experimental area was burned in August and seeded in October, 1940. On the bases of soil, topography, native vegetation, and the results of species trials conducted nearby, 17 lbs per acre of the following species mixture was used: *Agropyron*⁶ 3 lbs, *Agropyron trachycaulum* (Link) Malte 2 lbs, *Agropyron smithii* Rydb. 1.5 lbs, *Arrhenatherum elatius* (L.) Presl 2 lbs, *Bromus inermis* Leyss. 2 lbs, *Elymus canadensis* L. 2 lbs, *Melilotus officinalis* (L.) Lam. 1 lb, *Phalaris arundinacea* L. 1 lb, *Poa bulbosa* L. 2 lbs, and *Poa ampla* Merr. 0.5 lb.

The seed was broadcast 3 times and covered by harrowing. An excellent stand was obtained on all sites in 1941. The stand was not grazed until after 1944 and then only lightly in occasional years.

In 1942, two 30 x 1 ft transects were established on each site. At intervals from then through 1948 the following data were collected: relative rating, number of plants per square foot, average

⁶ From a commercial lot of crested wheatgrass containing both *A. cristatum* (L.) Gaertn. (fairway wheatgrass) and *A. desertorum* (Fisch.) Schult. (crested wheatgrass).



FIG. 3. Floral and height characteristics of *Agropyron cristatum* (L) and *A. desertorum* (R).

height, average diameter, vigor, and distribution. Herbage weights were estimated in 1942, 1944, and 1946. Herbage was clipped in 1953, 1954, and 1959. In 1954, data were also collected on density and height of each species. In 1956, 2 additional belt transects were established on each site and the following data recorded: basal areas of "crested wheatgrass"⁷ and of secondary species, herbage yields of "crested wheatgrass" and secondary species, and number of seed heads produced by "crested wheatgrass."

In 1956, 2 distinct species of crested wheatgrass, as distinguished by Konstantinov (1922, 1923), Peto (1929, 1930), Hay (1939), Knowles (1955), and Sarkar (1956), were observed on each site. Twenty plants of each type were dug in the spring of 1959 and planted at Utah State Univ. Chromosomes in pollen grains were counted. On the bases of head and seed characteristics and leaf pubescence of species confirmed by chromosome counts, plants in the field

⁷"Crested wheatgrass" refers to the mixture of *Agropyron cristatum* and *A. desertorum* before species determination was made.

were identified as to species of *Agropyron*. Species determinations were made on four 9.6 sq ft samples on each of the 3 sites.

Root yields were determined from 4 one-tenth cubic ft sub-samples taken at one foot intervals in each soil pit. To compare certain root characteristics of the 2 *Agropyron* species, a vigorous plant of each was dug. The plant crowns were 3½ in. in diameter. Plants were trimmed to a 4 in. root depth and one inch stubble height and grown in fine sand in the greenhouse in subirrigated containers. After 3 months they were removed, photographed, and measured. The stems and regenerated first-order roots were counted. After study of the branching habits of comparable root segments of each species, the root systems were washed, oven-dried, and weighed.

RESULTS

Shoots

The 2 types of crested wheatgrass plants were identified as *Agropyron cristatum* and *A. desertorum* (Fig. 3). The 20 plants collected to represent *A. desertorum* were tetraploids ($2n = 28$). Of the 20 collected to represent *A. cristatum* 19 were diploid ($2n = 14$) and one was tetraploid. Table II gives the density of plants of

TABLE II. Density of *Agropyron cristatum* and *A. desertorum* on each site in 1959 (plants per 9.6 square feet)

Sample	LOWER		MIDDLE		UPPER	
	<i>Agropyron cristatum</i>	<i>Agropyron desertorum</i>	<i>Agropyron cristatum</i>	<i>Agropyron desertorum</i>	<i>Agropyron cristatum</i>	<i>Agropyron desertorum</i>
1.....	38	2	19	16	5	16
2.....	37	3	20	28	1	12
3.....	29	1	12	17	10	9
4.....	30	1	16	17	6	10
Average.	34	2	17	20	6	12

each species on each site in 1959. *A. desertorum* comprised 6% of the wheatgrass on the lower site, 54% on the middle and 67% on the upper site. Since species determinations were not made until 1959, all vegetation measurements and references to "crested wheatgrass" are reported as *A. cristatum* plus *A. desertorum*.

In addition to differences in density of the 2 *Agropyron* species on each site (Table II), growth characteristics, ground cover, and total yield were also different on each site (Tables III and IV, Fig. 4). Leaf and flower stalk height and size of individual plants increased from the lower site to the middle and upper ones. The number of seed heads of "crested wheatgrass" (presumably mostly *A. cristatum*) on the lower

TABLE III. Average density (plants per 30 square feet) in 1954 and average basal area (per cent $\times$ 100) in 1956 on three sites

Species	LOWER ¹		MIDDLE ¹		UPPER ¹	
	Plants	Basal area $\times$ 100	Plants	Basal area $\times$ 100	Plants	Basal area $\times$ 100
	Density	Per cent	Density	Per cent	Density	Per cent
<i>Iva axillaris</i> Pursh....	52	11.8	—	—	—	—
<i>Rosa</i> sp. L.....	2	1.4	—	—	—	—
<i>Geranium</i> sp. L.....	1	1.8	—	—	—	—
<i>Bromus inermis</i> Leyss..	8	1.8	4	(T)	—	—
<i>Poa ampla</i> Merr.....	4	(T)	5	1.4	—	—
<i>Agropyron cristatum</i> + <i>A. desertorum</i>	154	1359.4	79	857.9	37	719.7
<i>Agropyron smithii</i>						
Rybd.....	48	25.2	7	11.0	5	(T)
<i>Bromus tectorum</i> L.....	3	3.2	10	7.2	5	2.3
<i>Poa secunda</i> Presl.....	—	—	7	16.7	T	(T)
<i>Elymus canadensis</i> L.	—	—	1	6.7	—	—
<i>Balsamorhiza sagittata</i> Nutt.....	—	—	2	7.4	3	3.2
<i>Tetradymia canescens</i> DC.....	—	—	1	3.0	1	(T)
<i>Collinsia parviflora</i> Dougl.....	—	—	T	(T)	T	(T)
<i>Chrysothamnus</i> sp. Nutt.....	—	—	—	—	2	3.0
<i>Artemisia tridentata</i> Nutt.....	—	—	—	—	1	3.0

¹ (T) equals less than a basal area of .01 per cent; T equals less than a density of one plant per 30 square feet.

site was approximately 4 times the number on the other 2 sites. Basal area of "crested wheatgrass" was 13.2, 8.3, and 7.0% on the lower, middle, and upper sites, respectively. The average density of "crested wheatgrass" was 5.1, 2.6, and 1.2 plants/sq ft on the lower, middle, and upper sites, respectively.

Average yield of crested wheatgrass on the lower, middle, and upper sites was 1403, 792, and 701 lbs/acre, respectively. Production was greatest in 1953, with an average of 1552 lbs/acre, less in 1954 and 1956 with an average of 1146 lbs/acre, and least in 1942, 1944, 1946, and 1959 with an average of 734 lbs/acre, oven dry weight (Table IV).

Responses of the minor species also varied with site (Table IV). The annual invader, *Bromus tectorum*, was excluded more rapidly on the 2 lower sites. *Bromus inermis* disappeared more rapidly from the middle and upper sites. On the lower site the production of *Agropyron smithii* and *Iva axillaris* increased during the study period, while *Agropyron spicatum* and *Melilotus* dropped out of the stand between 1942 and 1944. *Poa bulbosa* and *Arrhenatherum* disappeared from all sites before 1954. *Artemisia tridentata* appeared on the upper site in 1954. Species having a creeping growth habit generally succeeded

TABLE IV. Oven-dry herbage yields (pounds/acre) of major and minor species

MAJOR SPECIES									
Species	Site	YEAR							Ave.
		1942	1944	1946	1953	1954	1956	1959	
GRASS									
<i>A. cristatum</i> +	L	1326	796	980	2387	1252	2073	1010	1403
<i>A. desertorum</i>	M	527	521	700	1075	758	1035	930	792
	U	374	280	700	1193	786	976	600	701
Average.....		742	532	793	1552	932	1360	867	

MINOR SPECIES									
Species	Site	YEAR							
		1942	1944	1954	1956				
GRASS									
<i>Bromus tectorum</i>	L	86	48	2	1				
	M	691	92	32	14				
	U	403	154	3	53				
<i>Bromus inermis</i>	L	196	396	24	5				
	M	98	15	7	2				
	U	44	3	0	0				
<i>Poa ampla</i>	L	61	44	36	7				
	M	66	36	42	30				
	U	0	2	0	0				
<i>Agropyron smithii</i>	L	9	44	102	190				
	M	0	0	12	5				
	U	T	3	2	4				
<i>Elymus canadensis</i>	L	463	206	0	0				
	M	31	2	61	55				
	U	18	4	0	0				
<i>Poa secunda</i>	L	0	0	0	0				
	M	0	0	16	29				
	U	0	0	5	0				
FORBS ¹									
<i>Balsamorhiza sagittata</i> .	L	—	—	0	0				
	M	—	—	112	98				
	U	—	—	14	40				
<i>Iva axillaris</i>	L	—	—	150	131				
	M	—	—	0	0				
	U	—	—	0	0				
<i>Geranium</i> sp.....	L	—	—	8	16				
	M	—	—	0	0				
	U	—	—	0	0				
SHRUBS									
<i>Rosa</i> sp.....	L	—	—	16	45				
	M	—	—	0	0				
	U	—	—	0	0				
<i>Tetradymia canescens</i> .	L	—	—	0	0				
	M	—	—	90	30				
	U	—	—	21	5				
<i>Chrysothamnus</i> sp.....	L	—	—	0	0				
	M	—	—	11	0				
	U	—	—	51	31				
<i>Artemisia tridentata</i> ...	L	—	—	0	0				
	M	—	—	0	0				
	U	—	—	102	0				
Total yield of minor species.....	L	815	488	336	394				
	M	886	143	383	263				
	U	465	159	198	129				

¹ Yields of forb and shrub species were not determined in 1942 and 1944.

better on the lower site and non-creepers did better on the upper.

About 100 yds from the lower site, both *A.*



FIG. 4. Vegetation on the lower (L), middle (C), and upper (R) sites 16 years after seeding. Major species are *Agropyron cristatum* on the lower site and *A. desertorum* on the upper. Vegetation on the middle site is a mixture of the 2 *Agropyron* species. Large bunchgrass on the middle site is *Elymus cinereus*.

cristatum and *A. desertorum* were seeded in separate row plots of a species adaptability trial from 1938 to 1943 and were cultivated until 1945. The species trial site is essentially the same as the lower site. *A. cristatum* has invaded many other plots, including those sown to pure *A. desertorum*, thus further supporting the relative site adaptation of the 2 species of *Agropyron* as indicated in Table II.



FIG. 5. Typical specimens of *Agropyron cristatum* (L) and *A. desertorum* (R) with roots and shoots regenerated during 3 months. The root systems are 41 and 51 cm long, respectively.

Roots

Specimens of the 2 wheatgrasses are compared in several external morphological characteristics (Figs. 5 and 6, Table V).

The most noticeable differences between the specimens and presumably between the species, are that *A. cristatum* has more numerous nodal roots, a greater concentration of roots in the upper portion of the system, and better development of the third-order rootlets. The *A. cristatum* root system also had greater spread but less depth than that of *A. desertorum*. Kittock and Patterson (1959) have shown that the depth of root penetration of *A. desertorum* seedlings was significantly greater than for *A. cristatum* seedlings.

Root yields obtained in the field showed the same relationship to site as did herbage yields. Total root production on the lower site was approximately twice that on the middle or upper sites (Table VI). In addition, yields of grass and other roots were greater on the lower site than on either of the other two. Total root yield and the yield of grass and other roots were similar on the middle and upper sites. On all sites, and at all depths but one, the yield of other roots was greater than the yield of grass roots. From 48-63% of the total root yield on all sites was in the surface foot of soil, approximately 56% on the lower and middle sites and 75% on the upper site. The concentration of roots in the surface foot on the upper site may be due to the restriction of root penetration by the well-developed B horizon at 14-30 in. This would contribute to the droughtiness of the site.

DISCUSSION

These data illustrate two important points: 1) each site represents a different environmental complex with a different productive potential, and

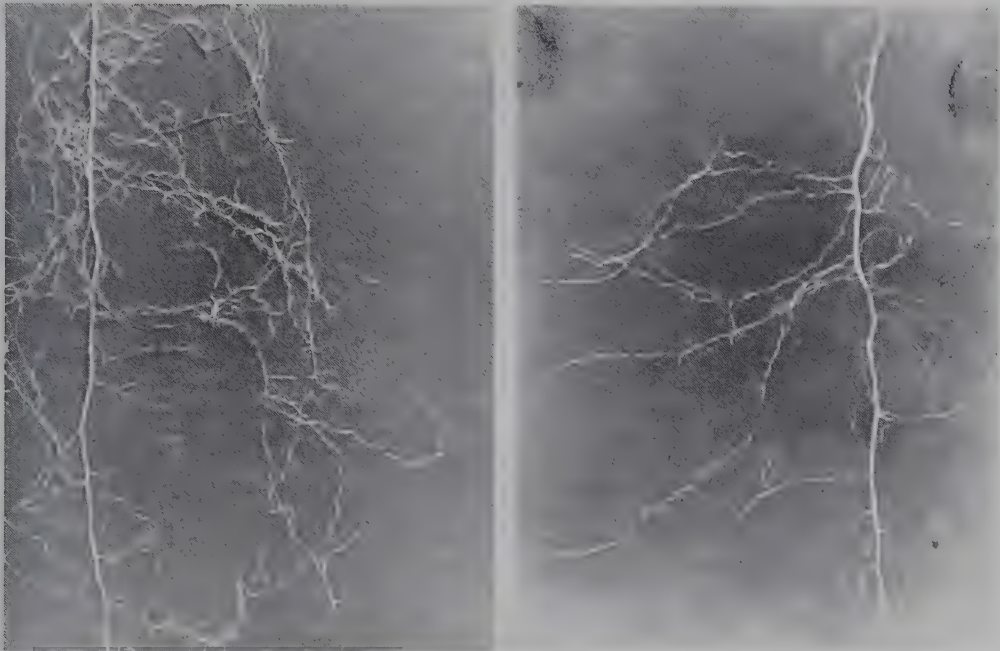


FIG. 6. Nodal root segments of *Agropyron cristatum* (L) and *A. desertorum* (R) from the 15 to 25 cm depth. Third order branches of *A. cristatum* are well developed; those of *A. desertorum* are weakly developed.

TABLE V. Gross anatomical comparison of typical specimens of two wheatgrasses grown from crowns

Criteria	Agropyron cristatum	Agropyron desertorum
<i>Shoot system</i>		
Crown diam., cm.....	9.0	9.0
Height, cm., avg.....	38	36
Weight, gm.....	17.9	17.3
Number of shoots.....	226	86
<i>Root system</i>		
Maximum depth, cm.....	41	51
Weight, gm., and (per cent)	23.96 (100)	15.85 (100)
Weight, 0-15 cm., gm. and (per cent).....	21.26 (89)	10.33 (65)
Weight, 15-25 cm., gm. and (per cent).....	1.54 (6)	2.05 (13)
Weight, 25-35 cm., gm. and (per cent).....	1.03 (4)	2.42 (15)
Weight, 35-46 cm., gm. and (per cent).....	0.13 (1)	0.83 (5)
Weight, 46-51 cm., gm. and (per cent).....	0.0 (0)	0.22 (1)
Number nodal roots.....	154	65

TABLE VI. Yield of grass roots and roots of other species on each site

Depth (feet)	LOWER		MIDDLE		UPPER	
	Grass	Other	Grass	Other	Grass	Other
^b Oven-dry pounds per acre-foot of soil						
0-1.....	4926	7904	3256	2487	3006	3390
1-2.....	1825	1201	1414	1536	653	884
2-3.....	960	1623	495	574	192	941
3-4.....	461	471	461	480	77	682
4-5.....	259	422	79	643	48	163
5-6.....	115	317	58	471	29	134
6-7.....	48	67	—	—	—	—
Subtotal.....	8594	12005	5763	6191	4005	6194
Site total.....	20,599		11,954		10,199	

2) *A. cristatum*, *A. desertorum*, and the other seeded species reacted differently on each site. The original seed mixture contained seeds of both species of crested wheatgrass; therefore *A. cristatum* and *A. desertorum* and the other species in the mixture were planted on each site. Because the area was grazed only occasionally after 1944, the established grasses had many oppor-

tunities to produce seed. Since 1941, the seeded species have either become established in the habitat where the environmental factors most nearly correspond to the requirements of the species are disappearing, or have disappeared from the stand because the environmental factors were not favorable for survival. Because determination of *Agropyron* species and density counts of *A. cristatum* and *A. desertorum* were not made until 1959, changes in dominance of the 2 species over the study period could not be determined. Perhaps germination and establishment of *A. cristatum* and *A. desertorum* varied initially on

each site or perhaps the dominance of one or both has changed gradually. In either case, site quality was responsible for the differences measured.

At sometime during the study, the density, basal area, and herbage yields of *Bromus inermis*, *Arrhenatherum elatius*, *Agropyron smithii*, *Iva axillaris*, *Geranium* sp., and *Rosa* sp. were greater on the lower site than on either of the other 2. The predominance of these mesic species on the lower site supports the soil evidence that it is the most mesic of the 3 sites.

The results have several implications to range management. *A. cristatum* and *A. desertorum* are better adapted to the sites than are any species seeded. Heinrichs and Bolton (1950) reported that *A. cristatum*, once established, is a strong competitor. The competitive ability of *A. cristatum* and *A. desertorum* undoubtedly accounts for the reduction in yield of most of the seeded and native species. *Agropyron smithii* is an exception. On the lower site it increased slowly until in 1956 it was by far the most prominent minor species (Table IV).

Since *A. cristatum* now dominates the lower site, apparently it is better adapted to more mesic conditions than is *A. desertorum* and is more competitive than *A. desertorum* on a mesic site. Conversely, since *A. desertorum* now dominates the more xeric upper site, apparently it is more drought tolerant and more competitive than *A. cristatum* on a dry site. On a site intermediate with regard to moisture, the species appear to be about equally adapted. To obtain maximum returns from a seeding investment and maximum competitive ability from a seeded species, range technicians must seed the species best adapted to a particular environment.

Native vegetation and soil are the range technicians' best guide for deciding which species to seed. In this study, native vegetation on the lower site consisted of robust *Artemisia tridentata*, *Elymus cinereus*, *Poa nevadensis*, *Stipa columbiana*, and small amounts of *Agropyron trachycaulum*. Similar vegetation, together with a Humic Gley or other soil with a high available moisture-holding capacity, indicate that a site is capable of supporting a vigorous stand of *A. cristatum*. For maximum competitive ability, *A. cristatum* should be seeded on areas similar to the lower site.

Native vegetation on the upper site consisted of *Artemisia tridentata*, *A. nova*, *Oryzopsis hymenoides*, *Sitanion hystrix*, *Poa secunda*, and *Agropyron spicatum*. Similar vegetation, together with a Brown soil, would indicate that a site is capable of supporting a vigorous stand of

A. desertorum. For maximum competitive ability *A. desertorum* should be seeded on areas similar to the upper site. Since most reseeding in the Intermountain West is done on Brown and Sierozem soils, *A. desertorum* would appear to be the species of choice from the standpoint of adaptability and life of stand.

Progress toward a more intensive range seeding program will depend partially on two factors: 1) development of vegetation-soil classification schemes that will permit range technicians to identify specific sites; and 2) introduction, development, and selection of species or strains adapted to specific sites.

SUMMARY

This study characterized 3 unlike adjacent sites and described the responses of several introduced grasses growing under these 3 sets of environmental conditions since 1941.

A range area was burned in August, 1940, and the following October a portion of the area was seeded to a mixture of grasses including a commercial lot of crested wheatgrass. On the bases of soil, native vegetation and slope, the study area was subdivided into lower, middle, and upper sites. Density, basal area, and yield data were taken by site and a root study was made. The soil on each site was described and chemical and physical determinations made. The soils of lower, middle, and upper sites were described as imperfectly drained Humic Gley, well-drained Humic Gley, and well-drained Brown soils, respectively. The available moisture-holding capacity of the soil profile decreased from the lower to the middle and upper sites.

Two different types of crested wheatgrass, noted on each site, were identified as *Agropyron cristatum* and *A. desertorum*. On the lower, middle, and upper sites 6, 54, and 67%, respectively, of the crested wheatgrass density was *A. desertorum*. Basal area, density, and herbage and root yields decreased from the lower to the middle and upper sites. *Bromus inermis*, *Arrhenatherum elatius*, *Agropyron smithii*, *Iva axillaris*, *Geranium* sp., and *Rosa* sp. were more important on the lower than on the middle or upper sites.

Root systems from sand cultures showed that *A. cristatum* had more numerous nodal roots, a greater concentration of roots in the upper part of the root system, and better development of third-order rootlets than did *A. desertorum*.

The data indicate that: 1) each site described represents a different environmental complex with a different productive potential, and 2) *A. cris-*

tatum and *A. desertorum* and the other seeded species reacted differently on each site.

The results have several implications to range management. *A. cristatum* and *A. desertorum* are better adapted to the sites described than are any of the other species seeded. Also, since *A. cristatum* now dominates the lower site, apparently it is better adapted to more mesic conditions than is *A. desertorum* and is more competitive than *A. desertorum* on a mesic site. Conversely, since *A. desertorum* now dominates the more xeric upper site, apparently it is more drought tolerant and more competitive than *A. cristatum* on a dry site. Since most seeding in the Intermountain West is done on the more xeric soils, *A. desertorum* would appear to be the species of choice from the standpoint of adaptability and life of stand.

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THE EFFECT OF GRAZING ON MARINE LITTORAL DIATOM POPULATIONS¹

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INTRODUCTION

During the colder seasons on the southern Oregon coast dark-brown carpets of attached

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diatoms form on the rock substrate of littoral slopes and tide pools. During summer these covers seldom appear except in the sublittoral. Frequently "bare" areas of various sizes occur in the upper half of the littoral zone and in mid-level and high-level tide pools. These areas lack visible algal covers but are usually densely populated by herbivorous littorines and limpets. Such undisturbed intertidal surfaces are almost devoid

of a measurable diatom population. During the summers of 1958-60, near Cape Arago (Lat. $43^{\circ} 20' N$), a dark diatom slick developed rapidly on most of these areas and on most other littoral substrate after all organisms had been removed by scraping and sterilization. The main purpose of the study in 1960 was to demonstrate the prime importance of grazers in maintaining this anomalous summer situation of high diatom reproduction rate and low standing crop.

This study attempted to measure quantitatively the diatom crop which developed in ungrazed areas and in areas where the number of grazers was controlled. In both cases screen closures were constructed for the experimental plots. This was part of a longer study of seasonal production changes in marine littoral and sublittoral diatoms.

The effect of grazing on sessile microvegetation has rarely been studied, either in marine or freshwater situations. Douglas (1958) noted an inverse relationship between the number of caddis larvae and numbers of the freshwater diatom *Achnanthes*. Brook (1952, 1954, 1955) showed that seasonal reduction of the freshwater diatom population on sand filter beds and macrophytes may be caused by the grazing activities of various insect larvae and even ciliate protozoans.

Moore (1938) and others described the ability of limpets to clear a "feeding" patch in an algal turf. Fischer-Piette (1948) studied the range and "prosperity" of *Patella* in relation to the abundance of algae. Test (1945) commented on the feeding habits of West coast species of *Acmaea*. North (1954) studied the erosive activities and metabolic efficiency of West coast *Littorina* but did not investigate the sources of food.

STUDY AREA

The study area is Yoakam Point, which extends northwestward as intertidal spurs alternating with long slot-like troughs. The sandstone promontory is less than one mile southwest of the Coos Bay entrance. The work area is a broad flat shelf at about the 6-8 ft tidal level and a nearly vertical wall extending from the +8 to -2 ft levels.

The Yoakam shelf was half covered by beds of *Mytilus californianus*. The inner half was largely covered by the red alga *Rhodomela larix* and some *Cladophora*. These algae were confined to moist depressions and conspicuous "bare" areas separated the algal "turfs" (Fig. 1a). The "bare" areas were usually populated with *Littorina scutulata* and small individuals of *Acmaea* spp. The littorines were generally clustered in depressions or cracks except on overcast days. Numerous



FIG. 1. Artificial tide pools carved in a sandstone shelf at Yoakam Point. a. View of the 6 pools and the surrounding "bare" area. Pools are numbered 1-6 from right to left; Pools 5 and 6 are screened. Trough-like natural pools may be seen in the foreground. *Rhodomela* "turf" and *Mytilus* beds appear in the background. b. Pools 6 and 5 on July 25, after removal of screens (Expt. 2, Table 1). Note the bare rock with littorines well dispersed in Pool 6. The density was about 7.1/dm². Pool 5, the control, is completely covered by a diatom slick about 3 mm in thickness.

shallow tide pools (usually less than 10 cm deep) were scattered amid mussel beds and *Rhodomela* "turf." *Odonthalia*, *Prionitis* and *Cladophora* were the most abundant algae in the pools. The "bare" rock between plants were dominated by *Littorina scutulata* and *Acmaea* spp. *Mytilus* was common in many pools. The lip of the shelf was exposed to severe wave action during most high tides; the broad flat top usually received only the wash.

The vertical wall used at Yoakam Point faces northeast and is exposed to the heavy wave action of combers running parallel to the wall. The zonation pattern is shown in Figure 2. Natural "bare" areas inhabited mainly by *A. digitalis*, *Balanus*, and tufts of *Endocladia* lie above the mussel bed from the 7-8 ft level and higher. Directly below the *Mytilus* is a narrow fringe of



FIG. 2. The vertical transect at Yoakam Point. a. The bare transect on June 23, 1960, soon after mounting the baskets. The upper plots (U) and lower plots (L) are numbered 1-4 from left to right. The approximate tide levels are indicated in feet above 0 tide mark. Some of the natural "bare" areas are marked with an x. The area marked with a Y is part of a vertical strip cleared more than a year before. b. The transect 16 days later. The dark diatom cover has become apparent from the base to the top of the upper baskets. Note the cover on the lower baskets. Two 6 x 6 inch squares have been cleared below these baskets. The bare streak on the right-hand side was caused by the abrasive action of algal fronds.

Odonthalia followed from the 5-1 ft level by *Iridaea*, *Hedophyllum*, and *Corallina*, all superimposed on a crust of *Lithothamnion*. "Bare" areas which interrupt the mussel beds are common (Fig. 2), and smaller "bare" patches often occur in the *Iridaea*-*Hedophyllum* area. *A. digitalis* dominates the "bare" areas above the 4 or 5 ft level. *A. pelta* and *A. scutum* are also common from below the 6 ft level to as low as 1 ft. Shotwell (1950) described the vertical zonation of *Acmaea* in a nearby cove on the Oregon coast.

Rock substrate not covered by macrophytes was also common in the sublittoral zone and the lowest parts of the littoral from Yoakam Point to Cape Arago (about 4 miles). Although gen-

erally covered by a crust of *Lithothamnion*, these areas were often clothed by patchy or continuous carpets of attached diatoms at any season. *Navicula* (*Schizonema*) *ramosissima* Ag., *N. (S.) grevillei* Ag. and *Licmophora abbreviata* Ag. were generally the dominant species. Relatively few herbivorous gastropods were present at these lower levels. *A. mitra* was regular but not common. Diatoms were also abundant as epiphytes in the lower littoral most of the year in some regions between Yoakam Point and Cape Arago. *Isthmia*, *Coscinodiscus*, and *Biddulphia* often completely clothed the branching red algae *Rhodomela* and *Odonthalia* when the latter were located in flat beds protected from heavy wave force. Very few grazers were present on these beds.

METHODS

Tide Pools

Six artificial tide pools, approximately 24 x 24 x 4.5 cm with a capacity of about 2.2 liters, were carved in the sandstone shelf at about the 6.5-7.0 ft tidal level, above the *Mytilus* zone (Fig. 1a). The pools were made with hammer and cold chisel; the bottom was smoothed with a wide-blade wood chisel. Eight to 10 holes ($\frac{3}{4}$ in. diam) were drilled around the lip of each pool. Plastic screw fasteners were set in each, and a stainless steel screen (8 mesh sq. in.) was secured over each pool by nickel-plated wood screws with thick rubber faucet washers. Each screen was molded around the edges with a light hammer to seal all openings. The mesh was fine enough to exclude almost all littorines. The screens could be rapidly removed and reset using the same mounts.

Various numbers of *Littorina scutulata* were introduced into bare, sterilized pools; pools without littorines served as controls. Sometimes littorines were introduced into pools that already had a diatom cover. All pools were screened and collections were usually made after 14 days. At that time littorines were removed, counted and their displacement volume determined. In most cases the dry weight was also determined. Any diatom cover was removed with a fine edge carpenter's scraper after the pool was drained. The remaining diatoms from bottom and sides were removed with absorbent cotton. The pools were then resterilized with 95% ethanol or absolute methanol, rinsed, and reused.

The abundance of diatoms was estimated by determining the absorbance of a methanol extract in a Beckman Model DU spectrophotometer at 665 m μ . The absorption maximum of chlorophyll

α in the red is close to 665 μ . Chlorophyll c is the only other pigment contributing to the absorption at this wavelength. All samples were frozen soon after collection, stored in darkness and extracted later. Comparison of fresh and frozen portions of the same material indicated that freezing had no observable effect on the absorption properties of the extract. Absolute methanol with 0.5% dimethylaniline was used as the solvent (Strain and Manning 1942). Ethanol or acetone did not effect complete extraction. The sample was extracted for 24-30 hr in darkness. The material was always damp when the solvent was added. Extraction was not complete if the sample was dry when solvent was added. Different volumes of solvent were used for samples of various size and dilutions were made when necessary so that no absorbance value was over 0.8. Serial dilutions of some extracts showed that Beer's Law applied to absorbance values of about 1.1 and below. Final relative absorbance calculations were based on a non-diluted 30 ml extraction. Corrections were made for the slight differences in area among the 6 pools. The results of a few tests indicate that a chlorophyll absorbance value of 1.0 may be equal to about 30 mg of diatom "organic matter" (weight lost on ignition). This ratio may change with season, species, or physiological condition of the plants.

Chlorophyll was used as the criterion of diatom mass because the collections included sand and cotton, which made it impractical to use weight. Cell counts could have been used, but the difference in cell volumes made such a technique too cumbersome.

Vertical Transect

Enclosures were prepared on the vertical wall to measure the effect of limpet grazing. A strip 1.2 m wide was cleared of all organisms from the one foot tide level to the top of the rock at about the 8 ft level (Fig. 2a). The rock was cleared by scraping and was sterilized with concentrated formalin.

Two rows of 4 stainless steel baskets were mounted at different levels. Each basket covered an area approximately 15 x 15 cm. The upper row (U) was at the 5 ft level; the lower row (L) was at the 3 ft level (Fig. 2). During all the experiments 2 plots were run as limpet-free controls and 2 were used for different numbers of *A. digitalis*, *A. pelta*, or *A. scutum*.

The same method of collecting and processing was used. The volume of whole limpets was taken as well as the dry weight of the shell-free

TABLE I. Tide pool experiments in which littorines were introduced into bare, sterilized pools. All data are based on 14 day periods. See text for additional explanation

Pool	Absorbance of diatoms @ 665 μ	No. of litt. per pool & type	Vol. of litt. per dm^2 (cm^3)	Dry wt. of litt. per dm^2 (g)	No. of litt. per dm^2	No. of dm^2 per litt.
Expt. 1 Mid-date 6-30-60						
6	1.29	0	—	—	—	—
5	.80	65 "shelf"	.29	—	8 $\frac{3}{4}$	.12
Expt. 2 Mid-date 7-16-60						
1	1.29	0	—	—	—	—
5	1.19	0	—	—	—	—
3	1.07	0	—	—	—	—
6	.02	62 "pool"	.35	.401	7.1	.14
1	.01	126 "pool"	.70	.787	14.4	.07
2	.03	122 "pool"	.70	.814	15.0	.07
Expt. 3 Mid-date 8-2-60						
5	2.22	0	—	—	—	—
6	1.83	12 "pool"	.09	.108	1.4	.73
4	1.52	6 "pool"	.05	.051	.7	1.45
3	.97	25 "pool"	.17	.172	2.9	.34
2	.33	36 "pool"	.21	.228	4.4	.23
1	.10	50 "pool"	.27	.286	5.9	.17
Expt. 4 Mid-date 8-15-60						
4	1.48	0	—	—	—	—
1	.61	12 "pool"	.09	.091	1.4	.71
2	.17	24 "pool"	.21	.210	2.9	.34
3	.04	36 "pool"	.28	.288	4.1	.24
Expt. 5 Mid-date 9-11-60 (pools unscreened)						
4	.01	Mixed	1.06	—	32.7	.03
5	.01	Mixed	.54	—	17.4	.06
3	.02	Mixed	.87	—	27.5	.04
1	.02	Mixed	1.08	—	32.9	.03
6	.02	Mixed	.32	—	8.6	.12
2	.03	Mixed	.68	—	22.8	.04
Expt. 6 Mid-date 9-25-60						
4	1.66	0	—	—	—	—
2	.22	36 "pool"	.25	—	4.4	.23

bodies. A plot was resterilized with 95% ethanol at the beginning of each experiment.

MAINTAINING DIATOM-FREE AREAS

Littorine Grazing

In the tide pool experiments littorines were introduced into bare, newly sterilized pools. The results appear in Table I and Figure 3.

Control pools invariably developed a thick carpet (0.5 cm) of diatoms on both bottom and sides in 12-16 days (Fig. 1b). The main source area of the diatoms was almost certainly the sublittoral region. In one experiment (Expt. 3,

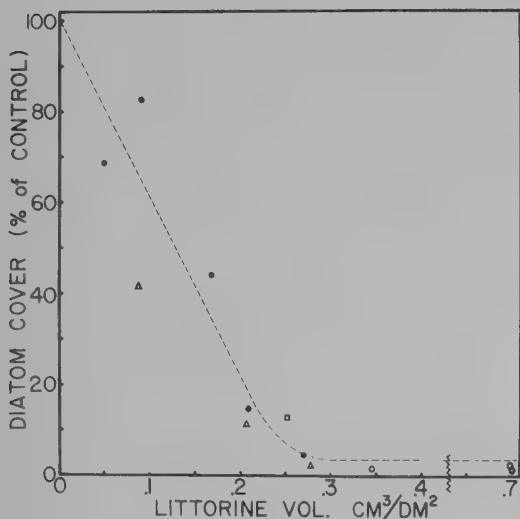


FIG. 3. The relationship between total littorine volume (not individual volumes) and the amount of diatom cover developed. In all cases littorines were introduced into bare, sterilized pools. The dashed line is for guidance. 0 = Expt. 2, • = Expt. 3, Δ = Expt. 4, $\square$ = Expt. 6 (Table I). See text for further explanation.

Table I) the screens of Pools 5 and 6 had not been cleaned and sterilized. As a result, the inoculation and appearance of a diatom cover was greatly accelerated. The flora in the ungrazed and grazed pools was similar and presumably no selective grazing occurred. *Stauroneis constricta* (Ehr.) Cleve, *Navicula ramosissima*, *Coscinodiscus* spp., and *Fragilaria striatula* Lyngbye composed the bulk of the material in decreasing order of abundance. Other diatoms made up the rest, almost to the exclusion of other groups of algae. None of the cells was very large and presumably all could be ingested or at least removed easily by *Littorina*. These species typified shallow tide pools at high levels where temperature fluctuations were great. The pools were usually flushed twice daily with 10-14°C water; however, at mid-day pool temperatures usually rose to 18-23°C unless the area was under fog. In deeper and consistently colder pools the diatom flora often differed considerably.

The first experiment in late June used about 8 littorines/dm² collected from the exposed shelf rock. After 2 weeks the rather dense population of littorines did not nearly succeed in maintaining a diatom-free area (Table I). Most of the snails in Pool 5 were aggregated along the walls and in the corners throughout the 2 weeks. Only the periphery was cleanly grazed. "Shelf" littorines were placed in tide pools and observed for short periods at other times. Invariably they moved

out of the pool entirely or clustered above the water line.

It became clear that littorines naturally inhabiting tide pools were necessary to obtain efficient grazing in a permanently submerged situation. In all cases when "pool" littorines were introduced into a bare pool they dispersed widely over the bottom and sides and remained spread throughout each experiment or until a diatom cover appeared. Besides the behavioral difference there was a definite size difference between the "shelf" and "pool" types. The mean volume of the "shelf" type was about .035 cm³; that of the "pool" was about .050 cm³. Very little overlap occurred and no morphological differences were observed. North (1954) demonstrated that smaller littorines were able to hang on wave washed rock better than larger ones; thus, the larger snails could be selected against, except in the greater protection of a tide pool.

The rest of the tide pool experiments involved the use of various numbers of "pool" littorines. In the second experiment (Table I) "pool" littorines of about the same volume and number as the "shelf" types used in the first experiment were able to keep Pool 6 essentially clear of diatoms. The great difference between Pool 6 and the control Pool 5 is shown in Fig. 1b. The results of all the experiments using "pool" types are combined and presented graphically in Figure 3. A pattern is easily recognized even though experiments are separated by almost 3 months. The relative absorbance values of diatom extract are given as percentages of the control in each case. Control values did not differ greatly throughout the study (Table I). In Figure 3 the total volume of littorines/dm² is used rather than the number of individuals/dm². With respect to diatom elimination, there appeared to be closer agreement between littorine volumes than between numbers (Table I). A plot using dry weight of littorines would produce a curve similar to that using volume. At present little is known about littorine range, feeding rate or scraping rate relative to animal size.

A total combined littorine volume of about 0.2 cm³/dm² (or about 0.2g/dm²) seems to be a critical value for the summer period (Fig. 3). A littorine volume above this value was invariably able to maintain a pool free of a visible diatom cover, at least over 2 weeks. Volumes below this value usually resulted in a patchy but quite apparent brown diatom carpet with relatively high chlorophyll values. In the latter case littorines were able to disperse throughout the pool during the first week of the experiment, but the entire

area was not covered frequently enough by the grazers, since small patches of diatoms developed during the second week. As these patches enlarged, the range of the littorines appeared to be correspondingly reduced. After 2 weeks each littorine was restricted to a cleared area of not more than a few cm^2 ; elsewhere a relatively thick diatom cover was present. Littorines were invariably within their small cleared areas. Apparently they did not traverse a diatom carpet but worked along its edges. Thus the feeding range (or total range of movement) was inversely related to the food supply and there was a vast difference between range on an essentially bare substrate and range in a carpet of diatoms. A "pool" littorine volume of over $0.2 \text{ cm}^3/\text{dm}^2$ (over 3 individuals/ dm^2) was apparently sufficient to range the entire area of the pool frequently enough to prevent the growth of diatom patches.

In mid-September the 6 sterilized pools were unscreened for 2 weeks, during which time there was free entry and exit of littorines and small limpets from the shelf and adjacent natural pools. No visible cover of diatoms developed in any pools. Chlorophyll values were similar to those obtained with littorine volumes of 0.35 to $0.70 \text{ cm}^3/\text{dm}^2$ in controlled experiments (Table I). The littorine volumes in the open pools were as high as $1.0 \text{ cm}^3/\text{dm}^2$ at the time of collection.

In June and early July the density of littorines on the Yoakam shelf was fairly low ($< 1/\text{dm}^2$). Pools 1-4 were unscreened at that time, and a heavy diatom cover developed in each within 2 weeks. Littorines were removed from the pools every second day but there were never more than 6 per pool. Several natural pools which had grazers removed in June developed a diatom cover before being invaded and eventually cleared.

The general lack of diatom cover in tide pools of the Yoakam shelf may thus be explained by the natural density of littorines in these pools, densities which generally exceeded $6/\text{dm}^2$. However, the question of the "bare" areas on the shelf itself remains. Occasionally in early summer, during periods of fog, a few diatom patches did develop in relatively moist areas. This was during a time of relatively low littorine density in the particular area ($1/\text{dm}^2$). If the "shelf" littorines were as effective grazers as the "pool" type it would be difficult to imagine a diatom cover developing during late July, August, September, or October. The density during this period was usually over $12/\text{dm}^2$. Even with few grazers an extensive diatom cover should probably not be expected during summer. The "bare" areas were at the 6-8 ft levels and were covered

TABLE II. Transect experiments in which limpets were introduced on bare, sterilized plots. All data (except Expt. 4) are based on 14 day periods. See text for additional explanation

Plot	Absorbance of diatoms @ 665 m μ	No. of limp. per plot & species	Vol. of limp. per dm^2 (cm^3)	Dry wt. of shell-free limp. per dm^2 (g)	No. of limp. per dm^2	No. of dm^2 per limp.
Expt. 1 Mid-date 7-2-60						
U-1	1.12	0	—	—	—	—
U-2	.04	10 A. dig.	1.51	—	4.3	.23
U-3	2.03	0	—	—	—	—
U-4	.08	10 A. dig.	1.42	—	4.3	.23
L-1	1.58	0	—	—	—	—
L-2	1.25	8 A. dig.	.97	—	3.4	.29
L-3	1.51	0	—	—	—	—
L-4	1.47	9 A. dig.	1.18	—	3.9	.26
Unscreened plot	3.37	0	—	—	—	—
Expt. 2 Mid-date 7-19-60						
U-1	3.10	0	—	—	—	—
U-2	2.00	2 A. dig.	.54	.083	.9	1.16
U-3	2.79	0	—	—	—	—
U-4	2.08	2 A. dig.	.43	.063	.9	1.16
Expt. 3 Mid-date 8-2-60						
U-1	1.14	0	—	—	—	—
U-2	.50	5 A. dig.	.56	.073	2.1	.47
U-3	.85	0	—	—	—	—
U-4	.13	5 A. dig.	.69	.093	2.1	.47
Expt. 4 Mid-date 7-25-60 (28 days)						
L-1	.32	0	—	—	—	—
L-2	.07	2 A. pelta	1.85	—	.9	1.16
L-3	.28	0	—	—	—	—
L-4	.08	2 A. pelta	1.81	.317	.9	1.16
Expt. 5 Mid-date 8-15-60						
U-1	1.97	0	—	—	—	—
U-2	.04	3 A. pelta	1.16	.202	1.3	.77
U-3	3.29	0	—	—	—	—
U-4	.09	3 A. pelta	1.03	—	1.3	.77
L-1	3.41	0	—	—	—	—
L-2	.02	4 A. scutum	1.29	.232	1.7	.58
L-3	3.18	0	—	—	—	—
L-4	.02	4 A. scutum	1.20	.195	1.7	.58

by water for only a few hours per day, sometimes by only one high tide. Even if the settled diatoms could withstand the hours of exposure, often to full sunlight, it is almost certain that their growth period would be limited to those few hours of high moisture as contrasted with the full daylight period in the pools. Probably relatively few effective grazers would be required to maintain a clear surface under these conditions.

However, during late October and early November (1960), extensive diatoms patches (primarily *Fragilaria*) developed on the "bare" areas

of the shelf, particularly near the artificial pools with their abundant source of inoculum. This development occurred during almost continually overcast conditions. At the time of observation large numbers of littorines were grazing at the edges of the patches. Whether the littorine population was low during the establishment of the patches or whether the "shelf" littorines were not effective enough to cope with the increased diatom production could not be determined. The winter situation will be discussed later.

Littorina scutulata ranged to at least the 11 ft level on the side of the Yoakam shelf. These last few feet of vertical rise were only occasionally covered by water or spray. The littorines of this "supra-littoral" fringe seldom contained diatom cells. It is unlikely that a diatom cover could develop at this level in summer even in the complete absence of grazers.

Limpet Grazing

The results of the limpet grazing experiments are presented in Table II and Figure 4. Dependence on favorable low tides limited the number of experiments on the Yoakam vertical transect. Tides after August were not adequate for continued work.

The development of a diatom cover after scraping and sterilizing the entire transect fol-

lowed a pattern observed several times in past years at the same location and in other intertidal stations in the Cape Arago region. In less than a week a dark diatom film appeared at the lowest levels and seemingly spread gradually upwards. After 2 weeks the dark slime cover had invariably spread to at least the 5.5 ft level (Fig. 2b) and eventually extended to the top of the transect. The apparent spread, however, was simply a reflection of differences in growth rate at different levels. Several days after sterilization diatom settlement had occurred at almost all levels. The lower portion of the transect was covered by water for longer periods allowing a longer growth period per day. Mortality rate during low tide exposure may have been higher in the upper portion.

Licmophora abbreviata and *Navicula ramosissima* were the first colonizers of the lower two-thirds of the transect; *Fragilaria striatula* was the successful slower growing diatom which covered the upper one-third. After 3 weeks various changes took place that may be referred to as "successional" events. These will be discussed later.

Acmaea digitalis was used at both the upper (U) and lower (L) levels for the first experiment (Fig. 2). The lowest natural occurrence of *A. digitalis* was about at the level of the upper series (5 ft). As a result, only the upper experiments demonstrated what was probably the grazing ability of these limpets (Table II and Fig. 4). In Figure 5a the upper plots with limpets are contrasted with the control plots. Figure 5b shows the limpets of a lower plot aggregated at the top. Only the upper portion of the lower plots had been grazed. It appears that a tendency on the part of the limpets to move upward allowed the development of a heavy diatom cover over the lower two thirds of the plots.

In the majority of the experiments there was closer agreement between total volumes than between total number of individuals with respect to diatom removal (Table II). Moore (1938) found that the size of the feeding area and the volume of the limpet *Patella* showed a more or less straight line relationship. Nevertheless, the 2 limpets in Expt. 2, which were almost equal in total volume to the 5 limpets in Expt. 3, were not as effective (Table II), indicating some limitations of large size.

The curve of Figure 4 indicates that a total combined volume of about $0.8 \text{ cm}^3/\text{dm}^2$ would be needed to maintain an area essentially clear of diatoms. However, only *A. digitalis* was used in volumes lower than this.

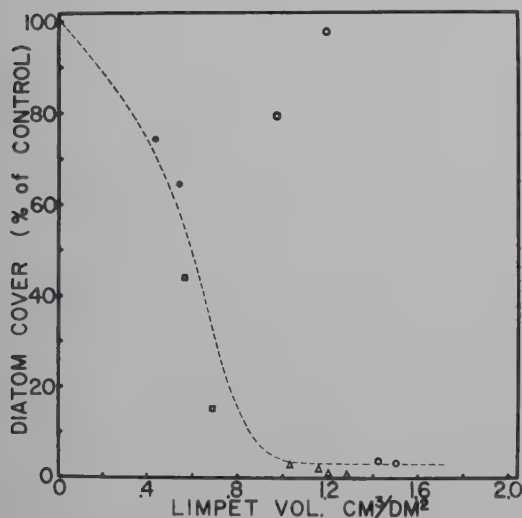


FIG. 4. The relationship between total limpet volume (not individual volumes) and the amount of diatom cover developed. In all cases limpets were introduced on bare, sterilized plots. The two upper points which are not in agreement represent the results of *A. digitalis* used below its normal vertical range. The dashed line is for guidance. 0 = Expt. 1, • = Expt. 2, □ = Expt. 3, Δ = Expt. 5 (Table II). See text for further explanation.

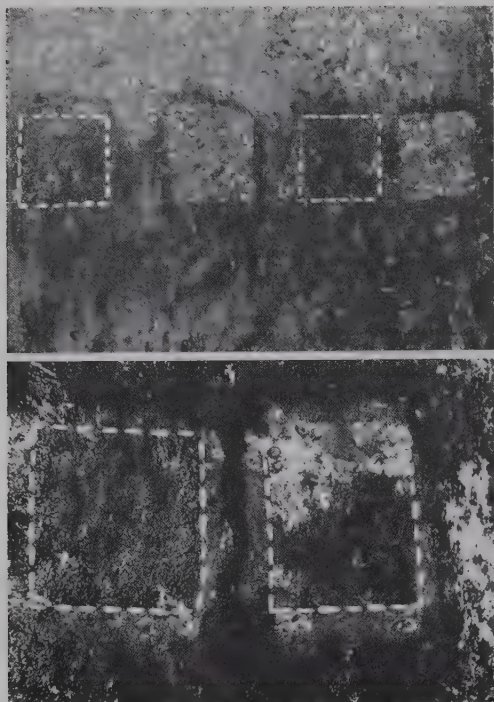


FIG. 5. Plots on the vertical transect on July 8, 16 days after sterilization and introduction of limpets. The baskets have just been removed. a. The upper series of plots. The control areas with a heavy diatom cover are outlined in white. Ten *A. digitalis* may be seen on U-2 and U-4. There is an almost complete absence of diatom cover. b. Two of the lower plots, L-3 and L-4. The control and the partly grazed plots are outlined in white. The 9 *A. digitalis* on L-4 are clustered near the top and only the upper third of the plot has been grazed. The black background is a continuous cover of diatoms.

The lower series was not as well used as the upper, since there was a period in mid-summer when diatom growth was poor even in the control plots. Because of these difficulties the lower plots were run for 4 weeks in mid-summer (Table II).

The last set of experiments began on August 7. *A. pelta* was used at the upper level and *A. scutum* at the lower. The volume and number were quite sufficient to preserve a clear area. It would have been desirable to use also a smaller volume and number of these species. Poor low tides during the remainder of the summer and fall prevented access. In all experiments except the first the limpets were collected from tidal levels equivalent to the level at which they were used.

Since a diatom cover was able to develop on

almost the full length of the transect, there is reason to believe that the natural "bare" areas described earlier were kept free of diatom covers by limpets. In fact, the density of *Acmaea* on the upper "bare" areas was greater than any used in the experiments. Many limpets on the natural areas were much smaller, however.

CLEARING A DIATOM COVER

The effectiveness of littorines and limpets in maintaining diatom-free areas has been demonstrated. How effective are these herbivores in clearing a well established diatom cover?

TABLE III. Tide pool experiments in which littorines were introduced into a 2 week diatom cover. They were allowed 7 days of grazing in Expt. 1 and 16 days in Expt. 2. See text for additional explanation

Pool	Absorbance of diatoms @ 665 mμ	No. of litt. per pool & type	Volume of litt. per dm ² (cm ³)	No. of litt. per dm ²	No. of dm ² per litt.
Expt. 1 Mid-date 7-2-60					
1.....	1.18	0	—	—	—
2.....	1.50	64 "pool"	.40	7.9	.13
3.....	1.14	0	—	—	—
4.....	.91	64 "shelf"	.25	7.3	.14
Expt. 2 Mid-date 9-18-60					
1.....	4.81	0	—	—	—
5.....	5.76	18 "pool"	.11	2.3	.44
3.....	4.72	36 "pool"	.29	4.2	.24
6.....	3.83	56 "pool"	.33	6.5	.15

In experiments summarized in Table III littorines were introduced into Pools 1-4 after a diatom cover had developed for 2 weeks in the absence of grazers. The addition of a large number of littorines ("pool" and "shelf" types) was ineffective in checking the increase of the diatom mat over 7 days. In one pool there was more diatom material than in the controls (Table III). In September littorines were again introduced into pools with a diatom cover and left for 2 weeks; even then they had little effect (Table III) but rather striking inroads were seen at the time of collection (Fig. 6). Cleared patches occurred around the edges, seldom in the center of a pool. The diatom carpet was very thick after 4 weeks and it was obvious that the littorines grazed at the edges only. Whether the same littorines would have eventually eliminated the diatom cover in these pools is not known. Diatom covers were allowed to develop in 6 natural pools on the Yoakam shelf in early summer. Within 4 weeks all pools had been cleared by the uncontrolled invasion of littorines and limpets. The



FIG. 6. Artificial pools 5 and 6 (back to front) after the last experiment (Table III). The heavy diatom cover has developed over a 4 week period and consists mainly of *N. ramosissima*. After a two week cover had developed 18 littorines were placed in Pool 5 and 56 in Pool 6. Conspicuous inroads may be seen, particularly in Pool 6. A diatom patch has also developed on the shelf rock in the foreground. It has been considerably reduced by littorine grazing. Large numbers of "shelf" littorines may be seen along the left-hand margin and elsewhere.

familiar peripheral invasion and constriction of the diatom mat was followed through this period.

No controlled experiments of a limpet attack on an established diatom mat were conducted; however, several observations were made at the Yoakam wall. The natural abundance of limpets increased steadily with increasing height. An invasion of limpets onto the transect from the undisturbed sides was followed during July and August. After 5 or 6 weeks, the diatom cover above the 4 ft level was eliminated by invading limpets, primarily *A. digitalis* and young, unidentified limpets.

THE EFFECT OF "SUCCESSION" ON DIATOM COVER

Although the elimination of a diatom cover in the upper littoral zone may be explained by the

activity of grazers, the disappearance of the cover in the lower littoral zone may occur in the complete absence of grazers, even during high diatom production. The normal sequence of events on the bare, sterilized vertical transect was described above. A cover first became evident on the lowest part of the transect, followed by the apparent upward extension through a 3 week period. However, after 4 weeks the lower portion of the transect was again bare from about the 3.5 ft level to the base at 1.0 ft. The 2 week cover in the lower control plots was also adversely affected. The disappearance occurred over 5 days. The cover of trailing *Navicula ramosissima* and *Licmophora abbreviata* disappeared except for a few isolated tufts of the former. The same puzzling phenomenon occurred in the summer of 1958 at the same location and was observed on other transects at Gregory Point in the summers of 1959 and 1960. Sometimes different diatom species were involved. In each case, there was no evidence of grazing.

It was first thought that the considerable wave action at high tides may have removed the heavy growth after it had reached an unstable thickness, yet this growth did not form a bound mat which could easily peel to leave bare rock behind. The cover at Gregory Point, a rather thin film of unicellular forms, was exposed only to light wave action, yet disappeared similarly. The even thicker carpets of *Navicula ramosissima* on sublittoral rocks exposed to very heavy wave action was further evidence against the hypothesis.

The elimination of the lower diatom carpet was best correlated with the appearance of young *Ulva* thalli on the same substrate. *Ulva* appeared commonly from about the 3-1 ft level. The density in this zone was about 1 plant/cm². Smaller thalli of *Ulva* also appeared from the 3.0-4.5 ft levels. The diatom cover in this area also lessened gradually through the succeeding 2 weeks. However, after maximum bareness in the lower portion of the transect at 4 weeks, there was a gradual recolonization and reestablishment of a diatom cover, different in aspect from the original. The new cover was a patchy thin film, composed primarily of *Fragilaria striatula* together with *Ulva*. There were also conspicuous increases in the scattered tufts of *Navicula ramosissima* which survived the first clearing at the 1-3 ft levels. The general successional pattern was *Licmophora abbreviata*-*Navicula ramo.* followed by *Ulva* and *Fragilaria*. This appeared not to be a type of seasonal progression, since the whole sequence could be repeated by resterilization at different periods during summer and fall.

Similar "successional" sequences have been observed in other temperate parts of the world (e.g., Wilson 1925, Bokenham and Stephenson 1938). It was common in the literature to find reports of a diatom cover succeeded by Enteromorpha or Ulva, and these followed by the array of red, brown, and green algae which normally inhabit the region.

The "successional" events were followed through the fall and winter of 1958-59. It became obvious that seasonal progression was being observed as much as succession. At many times during these months the lower part of the transect was free of diatom cover; at other times a patchy cover developed among the young macroscopic algae colonizing the surface. There have been several reports of algal inhibitory factors, often quite specific, which affect algae other than those producing them. Studies of planktonic algae have shown that an antibiotic principle may accumulate to toxic levels in the mass of water or in the culture medium (e.g., Sieburth 1960; Proctor 1957). If the increase in Ulva inhibited the existing diatoms, it might have been caused by a "leachate" derived from the Ulva which spread through the diatom mat during low tide exposure. If metabolites are involved, more probably an autoinhibitor produced by the diatoms accumulated to toxic levels in the thick carpet. Pratt and Fong (1940) and others have demonstrated autoinhibition in aging algal cultures.

DISCUSSION

These experiments and observations show that a heavy diatom cover develops in summer on rock substrate through most of the littoral zone when grazers are absent or reduced in numbers. However, on high littoral rocks exposed to direct insolation little diatom production could be expected regardless of gastropod density. This would be particularly true on horizontal surfaces, such as the Yoakam shelf. Experiments (Castenholz, unpublished) concerned with zonation at Gregory Point have shown that the upward extension of diatoms is most severely restricted on rock faces which receive direct insolation during low tide exposure (on south, east and west faces). Much depends on whether cloudless or overcast days are prevalent and on the time of low tides. In regions of potential diatom growth there is an apparent production gradient which shows increasing rate with decreasing tidal level. This is presumably due to differences in number of growth hours per day and in mortality rate. The gradient in undisturbed areas would appear super-

ficially even steeper, since there is a reverse gradient in grazer density.

The situation in winter was somewhat puzzling at first. The same rocks of the upper half of the littoral zone that were bare in summer were often largely covered by extensive diatom slicks. Diatom production rates on the horizontal shelf at Yoakam Point were, nevertheless, not as great as on suitable intertidal substrate in summer when grazers were removed. Yet, winter rates on the shelf were generally higher than contemporaneous rates on permanently submerged substrates in Coos Bay and on vertical littoral transects at Gregory Point (Castenholz unpublished). The rates in the last 2 areas were considerably lower in winter than in summer during 2 successive years. On horizontal exposed substrates, such as the high Yoakam shelf, the overcast winter conditions were probably responsible for a great reduction in diatom mortality and a lengthening of the daily growth period, allowing growth where little or none was possible during the desiccating conditions of summer.

The winter diatom covers appeared in areas with generally large populations of littorines and limpets. In summer, areas of potentially high diatom growth, are normally kept free of diatoms by grazer activity. Why, then, are these same areas and also higher areas not kept diatom-free in winter?

A few possibilities exist. Littorines and limpets may simply be less active in winter. Their range of movement may be considerably reduced. There is no evidence for or against this hypothesis. As another possibility, littorine numbers may be greatly reduced in local areas for a short time by the frequent winter storms. If this were true, diatom patches could begin to develop. It was shown above that once a diatom cover is established, littorines have considerable difficulty in removing it. There is some evidence to support this explanation. On a few occasions, after storms, areas of reduced littorine density were observed. At three times during the winter of 1960-61 (Jan., Feb., March) a large area of the Yoakam shelf (about 3 m²) was sterilized, effectively removing the large littorine population. Initially there was no measurable diatom cover. It is presumed that at least several days passed before a high littorine density was reestablished. After 2 weeks there was a sizable littorine population but only a barely perceptible diatom cover. Nevertheless, after 4 weeks, a thick diatom carpet (*Melosira* sp.) covered the area and the littorines were restricted to the edges of this mat. It is possible that the few days of low littorine density

were sufficient for diatoms to become established and that thereafter the littorines were not able to suppress the development and extension of this cover. Similar results were obtained on all 3 occasions. The frequent storms of late fall and winter could provide similar circumstances.

Something of a double anomaly exists in parts of the intertidal: in summer a high diatom reproduction rate with a small standing crop, in winter a somewhat lower reproduction rate but with a large standing crop. This type of situation should interest those workers who describe situations by assuming that the magnitude of the standing crop is a simple reflection of production rate. Aleem (1950) described the seasonal populations of British marine littoral diatoms. His frequent references to the disappearance of diatoms from rocks in summer lead me to suspect that grazing may have been involved; however, he made no reference to the animals inhabiting the study areas.

The significance of scraping and sterilizing in addition to the removal of grazers was not thoroughly treated in this study. Most of these experiments included this treatment. Is there anything intrinsically inhibitory to diatom growth on an unscraped, unsterilized surface? The problem of "succession" is again raised. It was observed that a diatom cover in the lower littoral may eventually succumb to "successional" events in the absence of grazers, leaving the rock substrate "bare" for various lengths of time. Also, if other algae are able to "replace" diatoms, then, are the natural "bare" areas amid a "mature" algal assemblage maintained in that state by the activity of grazers or the presence of algae, or both? It was observed many times that an area within the sweep of a larger algal thallus was easily kept free of cover by simple abrasive action. These are not the areas in question. In late June, 1960, 8 shallow tide pools near the seaward tip of Yoakam shelf were treated as follows: 2 were scraped and sterilized with formalin after the removal of grazers; 2 were merely sterilized after the removal of grazers; 2 were denuded of grazers, and 2 were left undisturbed. Within 3 weeks all but the undisturbed pools had developed a complete diatom cover. During this time invading grazers were removed periodically. In the summer of 1958 the removal of limpets from an upper portion of the vertical wall at Yoakam also resulted in the development of a diatom cover. These trials support the hypothesis that "bare" areas may be maintained by grazers alone.

This study has emphasized the effect of grazing on diatom populations. Little information was

obtained on the actual feeding habits of littorines and limpets. The effect of gastropod activity was the removal of diatom cells. Whether most of these cells were simply removed by the radula and lost or whether they were ingested and utilized was not determined. The digestive tracts of both limpets and littorines in all experimental plots were packed with diatoms to the exclusion of other material. Limpets and littorines collected from areas of potential diatom cover also contained primarily diatom cells, but other unidentified material was present. One may presume, that the primary food of these gastropods is diatom material. Only in the "supra-littoral" fringe were the littorines and limpets devoid of diatoms. Blue-green algae may be the principal food at this level.

SUMMARY

1. A virtual absence of epilithic diatoms in the upper and mid littoral of the southern Oregon coast was noted during 3 successive summers; however, on bare and sterilized littoral rock substrate thick diatom slicks developed within 2 or 3 weeks. Diatom production rate appeared very high in summer but most rock areas were kept diatom-free by herbivorous gastropods.

2. Six artificial tide pools of equal dimensions carved in a high intertidal sandstone shelf were screened and used as closures for controlling numbers of *Littorina*. Stainless steel baskets were anchored against a vertical wall in the littoral for similar experiments with *Acmaea*. Most experiments introduced known numbers and volumes of littorines or limpets into bare, sterilized pools or baskets to measure their relative abilities in maintaining diatom-free areas. Other experiments measured the effect of littorines on established diatom covers. Diatom crop, in all cases, was estimated by quantitative measurements of chlorophyll.

3. Results in summer show that a total littorine volume greater than $0.2 \text{ cm}^3/\text{dm}^2$ (or about 3 littorines/ dm^2) was adequate to keep an area nearly free of diatoms for 2 weeks. Normal densities in natural tide pools were several times this value. Volumes of less than $0.2 \text{ cm}^3/\text{dm}^2$ allowed diatom patches to develop. As these patches grew in size, each littorine's grazing range was progressively diminished until only the edges of the patches were grazed. A much larger volume of littorines and many weeks would be required to clear a previously established diatom cover. Limpet volumes over about $0.8 \text{ cm}^3/\text{dm}^2$ were required to maintain a diatom-free area. Numbers depended on the size and species.

The normal limpet population on "bare" areas in the upper littoral may equal or exceed this critical value.

A diatom cover may disappear from rocks of the lower littoral without the activity of grazers. "Successional" events may be involved.

4. Results of general seasonal observations indicate that a heavy summer diatom population is held in check by littorines and limpets in most of the upper half of the littoral, and by unfavorable factors of exposure in the very high littoral or "supra-littoral" fringe. The potential for diatom production increases as vertical level decreases. Large diatom populations in winter in the upper littoral and "supra-littoral" may be due to frequent storms causing temporary reductions in littorine densities at which time diatom covers may become established. It is also possible that littorines and/or limpets are less active during winter.

5. Diatoms probably constitute the principal food material of *Littorina scutulata* and most epilithic species of *Acmaea* in the littoral zone. However, the amount of diatom material removed from rock may reflect a considerable amount lost by radular scraping as well as that ingested.

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RELATIONSHIPS BETWEEN PLANTS AND SOILS OF FOUR RANGE PLANT COMMUNITIES IN SOUTH TEXAS¹

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Distinct plant communities occur in South Texas and the narrow transitional zones between them suggest that local edaphic conditions may be limiting factors in vegetational distribution. The South Texas plant communities not only differ in their floristic composition, but also in productivity, and in their economic returns to landowners. An understanding of the factors regulating potential production and distribution of

range plants is needed for the management of these native lands. Unfortunately, basic ecological data are not available for most of these rangelands.

The purpose of this study was to evaluate the vegetational resources of 4 important South Texas plant communities and to isolate factors that may contribute to plant distribution and abundance. Plant communities selected were representative of large areas of South Texas rangeland. These were (1) a mesquite-buffalo grass community, (2) a chaparral-bristleglass community, (3) a bunchgrass-annual forb community, and (4) a prickly pear-short grass community.

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The study area was on the Rob and Bessie Welder Wildlife Foundation Refuge, San Patricio County, Texas, which is approximately 8 miles northeast of Sinton on U. S. Highway 77. The specific area of study was that portion of the Refuge known locally as the "Lake Pasture."

A preliminary study of the vegetation of the Refuge was made in 1956 and general descriptions of the sites and communities were given by Box (1957). Detailed field investigations and laboratory analyses were carried out in 1957, 1958, and 1959 for this study. Portions of this work were presented to the graduate school of the Agricultural and Mechanical College of Texas in partial fulfillment of the Ph.D. degree.

The Rob and Bessie Welder Wildlife Foundation, Sinton, Texas, provided funds, equipment, and the research area for the study. It was directed by personnel from the Department of Range and Forestry, the Agricultural and Mechanical College of Texas. Dr. Vernon A. Young suggested and directed the study and many helpful suggestions were made by Drs. Robert A. Darrow, Curtis L. Godfrey, Frank W. Gould, Wayne C. Hall, Omer E. Sperry, Gerald W. Thomas, and O. C. Wallmo. Special credit is due to Dr. Clarence Cottam and Mr. Caleb Glazener of the Welder Foundation staff for their encouragement, interest, and assistance.

DESCRIPTION OF THE AREA

The study area was in a somewhat transitional zone between the Coastal Prairie and the Rio Grande Plain vegetational regions. This intermediate location is reflected in the flora and fauna which comprise many species of both regions. Approximately 1300 species of flowering plants have been reported from the area (Rowell 1957) of which more than 200 are grasses (Gould and Box 1959).

Climate

The climate is characterized by relatively warm temperatures in all seasons. The winters are generally short and mild. Long periods of high temperatures in summer are common, with several weeks with temperatures near 100° F to be expected. At Beeville, just north of the Refuge, the recorded temperature extremes are 106° and 5° F. At Corpus Christi the extremes are 105° and 11° F. Computed over 40 years, mean temperatures at Beeville range from 55.3° F in Jan. to 83.8° F in July. On the average, frosts occur between Dec. 2 in the fall and Feb. 22 in the spring. The average length of the frost free period at the Beeville station in 283 days (Norquest 1941).

The average annual rainfall for the general area is near 30 in. with averages for the principal stations as follows: Sinton, 30.62 in.; Woodsboro, 31.87; Corpus Christi, 25.84; Beeville, 30.81; and Austwell, 33.89 in. In 1956, Sinton received only 19.79 in. of total rainfall. The Refuge area had an average rainfall of 41.75 in. for 4 stations in 1958.

Soils and land use

The predominant soils are dark, calcareous to neutral clays and clay loams. The main series represented on the upland are Victoria, Monteola, and Orelia (Oakes *et al.* 1958). The bottomlands are generally characterized by brown to dark gray calcareous clays and clay loams mainly of the Leona, Frio, and Lomalto series. In the general area surrounding the Welder Refuge the clay and clay loam soils are used for pasture and for the production of cotton, grain sorghums, and vegetables.

Large areas of eolian sand are present. These are primarily of the Nueces and Zavala series. These soils are used for grazing since severe wind erosion results when they are not protected by a permanent vegetative cover.

Throughout the period of recorded history, the study area has been used for livestock production, and has always supported moderate to heavy populations of deer and other wild animals. During this study it was stocked with Hereford steers at the rate of one animal unit to each 13.5 acres. About one adult white-tailed deer was present for each 7 acres, giving a stocking rate of one animal unit for each 10.25 acres for deer and cattle combined.

VEGETATION

The vegetation of the Refuge is part of the grassland climax that occurs along the Gulf of Mexico. This grassland has been called the Coastal Prairie by Weaver and Clements (1938).

Early explorers and naturalists described the area as a veritable sea of grass with trees only on the watercourses (de Solis 1767, Newell 1838, Havard 1885). Today woody species occur on all soils except the deep eolian sands.

The southern portion consisted of a short grass prairie with heavy stands of running mesquite (*Prosopis juliflora* var. *glandulosa*).³ This area was called a mesquite-buffalo grass community.

The central portion was covered with a complex of South Texas chaparral consisting of low growing brush, of which the major species were blackbrush (*Acacia amentacea*), lote bush (*Con-*

³ Plants names are those used in Rowell 1957, and Gould and Box 1959.

dalia obtusifolia), brazil (*Condalia obovata*), prickly ash (*Zanthoxylum fagara*), granjeno (*Celtis pallida*), and agarito (*Berberis trifoliata*). This area was called a chaparral-bristlegrass community.

Large areas of eolian sand occurred throughout the northern portion of the Lake Pasture. These areas contained dense stands of seacoast bluestem (*Andropogon scoparius* var. *littoralis*), balsamscale (*Elyonurus tripsacoides*), and other grasses. Forbs were particularly evident, the spring aspect appearing like a pure stand of annual plants. This area was called a bunchgrass-annual forb community.

Areas covered with dense stands of prickly pear (*Opuntia lindheimeri*), chaparral, and mesquite occurred on clay loam sites. This vegetational type was called a prickly pear-short grass community.

The study area was stratified into 4 plant communities on the basis of the characteristic vegetation. Twenty sampling stations were located at random within each vegetational area. Species composition of herbaceous plants was determined from data collected from two 50-ft line intercepts, as described by Canfield (1942), at each station. Brush cover was recorded on each transect. The end points of the 50-ft transects were used as points for analysis of vegetation density by distance measurement methods (Cottam and Curtis 1956).

Vegetational attributes were subjected to an analysis of variance to determine if real differences existed between communities. Significant differences at the .05 level were demonstrated between grass cover, total brush cover and mesquite cover in the communities studied.

Herbaceous vegetation

The most abundant grasses on the mesquite-buffalo grass community were buffalograss (*Buchloe dactyloides*), 3 awn grasses (*Artistida* sp.), filly panic (*Panicum filipes*), plains bristlegrass (*Setaria macrostachya*) and curly mesquite (*Hilaria belangeri*). The most abundant forbs were small croton (*Croton nonanthogynus*), horsemint (*Monarda punctata*), and prairie cone-flower (*Ratibida columnaris*). The most common grasses on the chaparral-bristlegrass area were plains bristlegrass, buffalo grass, curly mesquite, 3 awn grasses and filly panic. The same forbs occurred on this area as on the mesquite type. Percentage composition data from 100 line intercepts studied in the summers of 1957 and 1958 are summarized in Table I.

The major grasses of the bunchgrass-annual

TABLE I. Comparison of the percentage composition of herbaceous vegetation (basal density) on four plant communities for the summers of 1957 and 1958

Species	Mesquite		Chaparral		Bunchgrass		Prickly pear	
	1957	1958	1957	1958	1957	1958	1957	1958
<i>Buchloe dactyloides</i>	29.2	30.4	24.8	25.9	—	—	8.3	14.3
<i>Panicum filipes</i>	14.2	16.1	6.6	5.5	—	—	3.9	0.7
<i>Artistida</i> sp.....	17.4	16.1	8.8	15.0	0.7	1.7	6.8	8.3
<i>Setaria leucopila</i>	12.8	11.8	29.8	16.8	—	—	18.8	11.1
<i>Panicum obtusum</i>	2.9	3.1	0.5	1.4	—	—	T	T
<i>Hilaria belangeri</i>	10.8	11.9	20.8	24.0	—	—	20.7	21.1
<i>Eriochloa contracta</i>	0.7	0.2	T	0.7	—	—	T	T
<i>Chloris verticillata</i>	2.2	2.6	0.7	4.5	—	—	22.5	27.5
<i>Cenchrus</i> sp.....	0.5	0.0	T	T	12.9	14.4	8.8	5.8
<i>Andropogon saccharoides</i>	2.2	0.1	0.1	T	—	—	T	1.0
<i>Setaria geniculata</i>	0.7	0.7	T	T	—	—	0.5	0.5
<i>Bouteloua rigidiset</i>	0.1	0.0	0.1	T	—	—	0.3	T
<i>Leptoloma cognatum</i>	0.3	0.0	T	T	1.8	2.3	0.2	T
<i>Trichachne californica</i>	0.3	0.0	0.8	T	—	—	0.2	T
<i>Paspalum hartwegianum</i>	0.7	0.0	0.9	T	—	—	0.7	0.5
<i>Bouteloua curtipendula</i>	T	T	0.1	T	—	—	T	T
<i>Stipa leucotricha</i>	T	2.0	0.1	1.5	—	—	0.2	1.6
<i>Tridens albens</i>	T	2.1	0.6	T	—	—	T	T
<i>Panicum fasciculatum</i>	T	T	T	T	—	—	—	—
<i>Tridens eragrostoides</i>	T	T	0.1	T	—	—	0.9	T
<i>Paspalum lividum</i>	T	T	0.3	T	—	—	T	T
<i>Andropogon littoralis</i>	—	—	—	—	12.1	29.2	—	—
<i>Brachiaria ciliatissima</i>	—	—	—	—	5.4	1.0	—	—
<i>Panicum firmulium</i>	—	—	—	—	18.5	21.0	—	—
<i>Chloris cucullata</i>	—	—	—	—	5.0	3.4	—	—
<i>Paspalum ciliatofolium</i>	—	—	—	—	2.4	6.4	—	—
<i>Bouteloua hirsuta</i>	—	—	—	—	1.3	2.3	—	—
<i>Elyonurus tripsacoides</i>	—	—	—	—	2.1	4.0	—	—
<i>Eragrostis oxylepis</i>	—	—	—	—	0.7	1.7	—	—
<i>Paspalum plicatulum</i>	—	—	—	—	0.7	T	—	—
<i>Sporobolus pyramidatus</i>	—	—	T	0.7	—	—	3.9	5.1
<i>Croton</i> sp.....	1.2	T	2.0	0.3	2.0	1.0	T	T
<i>Ruellia</i> sp.....	0.7	0.4	0.6	1.5	—	—	T	T
<i>Acacia angustissima</i>	0.4	T	0.4	T	—	—	T	T
<i>Gutierrezia texana</i>	0.2	T	0.2	T	—	—	0.1	0.8
<i>Euphorbia</i> sp.....	0.3	T	0.6	T	—	—	T	T
<i>Phyla incisa</i>	T	T	0.1	1	0.1	0.4	T	T
<i>Ratibida columnaris</i>	0.9	0.9	T	0.5	—	—	T	T
<i>Monarda punctata</i>	0.2	0.9	T	1.2	—	—	T	T
<i>Commelina erecta</i>	T	T	0.3	T	0.5	1.0	T	T
<i>Verbesina enceloides</i>	—	—	—	—	15.6	T	—	—
<i>Nama hispidum</i>	—	—	—	—	9.2	4.0	—	—
<i>Eriogonum multiflorum</i>	—	—	—	—	1.8	1.0	—	—

forb community were seacoast bluestem, knotroot panic (*Panicum firmulium*), sand bur (*Cenchrus* sp.), fringeleaf paspalum (*Paspalum ciliatofolium*), balsamscale, and hooded windmill grass (*Chloris cucullata*). The most common forbs were skunk daisy (*Verbesina enceloides*), large croton (*Croton capitata*), rough nama (*Nama hispidum*), heartsepal wild buckwheat (*Eriogonum multiflorum*), and bull nettle (*Cnidoscolus texanus*). Woody species and prickly pear did not occur here.

Most abundant grasses in the prickly pear-short grass community were windmill grass (*Chloris verticillata*), curly mesquite, sandburs, plains bristlegrass and buffalo grass. Forb density was low; the major species included broomweed (*Gutierrezia texana*), wild petunia (*Ruellia* sp.), and small croton.

Grasses of the general area were of tropical origin and of the Panicoid and Eragrostoid-Chloroid lines (Box and Gould 1958).

Woody vegetation

The most noticeable differences between the 4 plant communities were the amount and kind of woody plants present. The woody cover ranged from dense stands of chaparral and prickly pear on the clay and loam areas to an almost complete absence of brush on the deep sands. Density of brush plants on each of the 4 communities is in Table II.

TABLE II. Density of woody plants on four range plant communities on the Welder Wildlife Refuge

Species	PLANTS PER ACRE			
	Mesquite-buffalo grass	Chaparral-bristlegass	Bunchgrass-annual forb	Prickly pear-short grass
<i>Prosopis juliflora</i> var. glandulosa.....	147.3	70.4	—	828.5
<i>Acacia amentacea</i>	1.1	78.3	—	22.6
<i>Acacia farnesiana</i>	20.4	15.6	—	5.4
<i>Acacia tortuosa</i>	5.6	13.7	—	5.4
<i>Condalia obtusifolia</i>	5.6	46.9	—	22.6
<i>Zanthoxylum fagara</i>	1.1	15.6	—	5.4
<i>Berberis trifoliata</i>	*	42.9	—	*
<i>Celtis pallida</i>	*	7.8	—	*
<i>Condalia obovata</i>	*	5.9	—	*
Total brush.....	181.3	312.2	—	904.5
<i>Opuntia lindheimeri</i>	*	*	—	172.3

* Less than one plant per acre.

Mesquite grew on all sites where brush occurred, but its density, canopy cover and percentage composition varied between sites. Approximately 95% of the brush cover on the mesquite-buffalo grass community consisted of running mesquite while it comprised only 10.9% of the total brush of the chaparral community. The prickly pear-short grass community had the greatest density of mesquite plants (80% of the canopy cover). The plants on the prickly pear community were small and switch-like, giving a high density with a low canopy cover.

Other brush species varied between communities. Blackbrush was the prominent shrub of the chaparral community, comprising 34.8% of the total canopy cover, yet it contributed only 1.9% of the canopy on the mesquite community and 2.6% on the prickly pear community. Total brush cover was essentially the same in all communities where brush occurred. The mesquite community had 18.56% cover, the chaparral community 20.44%, and the prickly pear community 18.80%. However, the prickly pear community had 20.60% of its area covered with the cactus,

making a total brush-prickly pear cover of 39.40% with brush and cactus combined.

Relationships between vegetational characteristics

Basal density of grasses, total brush canopy cover, mesquite canopy cover, percentage of climax plants present and litter present were measured at 20 locations within each community. The per cent of climax plants at each site was determined by comparing the per cent composition at each location with the theoretical climax developed by Box (1957) from relict areas on each site.

The vegetational properties of each community were correlated with each other in an attempt to show relationships between plant attributes of each community. A summary of the correlations is in Table III.

TABLE III. Correlation coefficients between vegetational properties of four range plant communities on the Welder Wildlife Refuge

Community	Brush cover	Mesquite cover	Range score	Brush acre ²	Litter
Mesquite-buffalo grass					
Grass cover.....	-.341	-.393	-.127	-.109	-.448*
Brush cover.....	—	.979**	-.109	.312	.441*
Mesquite cover.....	—	—	-.067	.369	.452*
Range score.....	—	—	—	.419	.483*
Brush/square acre.....	—	—	—	—	.433*
Chaparral-bristlegass					
Grass cover.....	-.513*	-.197	-.526*	-.056	-.497*
Brush cover.....	—	.527*	.420	.156	.063
Mesquite cover.....	—	—	.004	.230	-.035
Range score.....	—	—	—	.098	.534*
Brush/square acre.....	—	—	—	—	.397
Bunchgrass-annual forb					
Grass cover.....	—	—	-.070	—	.043
Range score.....	—	—	—	—	-.449*
Prickly pear-short grass					
Grass cover.....	-.156	-.388	-.418	.344	-.234
Brush cover.....	—	.591**	.394	.078	.276
Mesquite cover.....	—	—	-.064	-.057	-.029
Range score.....	—	—	—	.046	.142
Brush/square acre.....	—	—	—	—	-.026

* r values greater than .433 are significant at the .05 level.

** r values greater than .549 are significant at the .01 level.

A highly significant positive correlation existed between total brush cover and mesquite cover in the mesquite-buffalo grass community. This was expected, since more than 95% of the total brush cover was mesquite. The only other significant correlations between vegetational properties in this community occurred between litter and other attributes. Litter was negatively related to grass cover and positively correlated with brush cover, mesquite cover, per cent of climax grasses and brush density. The positive correlations between brush and litter were attributed to the large amount of unpalatable leaves dropped an-

nually by brush plants. It appeared unusual that litter would be negatively correlated with grass density and positively related to per cent of climax grasses or range score. This condition existed, however, since the area was subjected to moderately heavy grazing and the largest percentages of climax plants remained under the protective canopy of the small running mesquite clumps. Likewise, grasses in the open areas were grazed heavily and little litter was deposited.

Similar relationships existed in the chaparral-bristleglass community; litter was negatively correlated with grass cover and positively correlated at the .05 level with per cent of climax plants. As in the mesquite community, climax grasses in the chaparral community were present in largest amounts under the protection of brush clumps. Total brush cover was positively related to mesquite cover in the chaparral community, but the relationship was not as high as in the mesquite community. Grass density in the chaparral community was negatively correlated at the .05 level to brush cover. It appeared that competition of the brush for light, moisture and space was limiting grass density in the brushy areas. In addition, buffalo grass and curly mesquite com-

prised the bulk of the grasses in open areas. These dense sod grasses were increasers or invaders on the site and did not contribute greatly to the climax vegetation. Climax decreasers made up only a small part of the total grass composition. This situation is reflected in the significant negative correlations between per cent of climax plants and gross cover on the chaparral community.

In the bunchgrass-annual forb community, the only significant relationships were negative correlations between litter and forb density and between litter and climax plants. Apparently less dry matter was produced by forbs than by grass, thus resulting in decreased litter. Climax grasses were grazed heavier than the invader plants and less litter was deposited under them.

The only significant relationship between vegetational properties on the prickly pear-short grass community was a positive correlation at the .01 level between total brush cover and mesquite cover.

No significant relationship existed in any community between brush density and total brush cover. Field observations confirmed that often the dense stands of small shrubs had a small



FIG. 1

canopy cover while scattered large shrubs had large canopies. Also in all cases forb density was negatively related to both grass density and brush density although these correlations were not significant at the .05 level.

In general, presence of brush reduced grass density, although this relationship was significant only in the chaparral community. The reduction of grass by brush appeared to be in the amount of canopy cover of the brush rather than in the density of woody plants. In no case did brush density have a negative correlation approaching significance with grass density or per cent of climax plants. The only significant decrease in grass due to brush influence was in the chaparral community where shading from the dense foliage is a factor.

SOILS

General description

The soils of the study area are principally of the Victoria series, over one-half of those on the Refuge being made up of Victoria clay alone. Coffey (1909), in a reconnaissance survey of South Texas, mapped the general area as a composite of Victoria clay, Victoria loam and Victoria fine sandy loam. Unpublished field notes from an official survey now under way (Soil Conservation Service 1959) showed Victoria clay, Monteola clay and Orelia clay loam as the principal soils of the uplands; and Neuces fine sand, Miguel loamy fine sand, Zavala fine sandy loam, and Leona clay as the most abundant soils in the lowland areas.

Soil profile descriptions

Soil profiles were described at each vegetation sampling location using the procedure outlined in the Soil Survey Manual (Soil Survey Staff 1951). In addition, profiles were examined in power line holes and pipe line ditches dug during the study. Little variation was noted between profiles within communities. Likewise, only small variations were noted between profiles of the mesquite-buffalo grass community and the chaparral community. Profiles under the bunchgrass community and the prickly pear community were different from the others. Soil series names were taken from an un-correlated soil survey (Soil Conservation Service 1959).

The Plymouth Oil Company (1957) made extensive oil explorations in the study area during the summer of 1957. Field logs for 75 seismograph holes were available from the company. In addition, observations of color and textural changes of the underground material were made

at each hole. The seismograph holes were at $\frac{1}{4}$ mile intervals over the study area and were drilled to 105 ft.

Studies of the soil and geological material indicated that the same deposits of marine clay were found under all plant communities. The clay layer was at a 3-4 ft depth in the mesquite and chaparral communities, but was at depths of 15-40 ft in the other communities. The average depth of the clay layer was 58.6 ft for the mesquite-buffalo grass community and 62.4 ft for the chaparral-bristlegrass community.

Color variations were noted throughout the profile. Layers of light gray, grayish brown, and pale yellow clay were found in the same holes. Apparently no relationship between color and depth existed. Likewise, position of the layer in the profile and color showed no relationship.

Mesquite-buffalo grass community

A typical profile from the mesquite-buffalo grass community is described below. Color names for the first 4 ft are standard Munsell color names; those below 4 ft are visual estimates.

<i>Depth</i>	<i>Victoria Clay</i>
0-22 in.	Very dark gray (10YR 3/1; black, 10YR 2/1 moist) clay; alkaline, pH 7.7-8.0; strong medium granular; very sticky and plastic when wet; calcareous; grades to horizon below.
22-43 in.	Dark gray (10YR 4/1) clay; weak medium blocky; very firm; sticky and plastic when wet; calcareous; grades to horizon below.
43-48 in.	Light brownish gray (2.5Y 6/2) clay; strongly calcareous; very firm; massive; contains small concretions of CaCO_3 ; 5-12 in. thick; transition to parent material below.
48 in. plus	Pale yellow (2.5Y 8/4) to white (2.5Y 8/2) clay; strongly calcareous; massive; very firm; contains small concretions of CaCO_3 ; may continue many feet deep.
4-40 ft	Light gray clay, very firm, massive, little change throughout the layer.
40-45 ft	Grayish brown, tan or pale yellow clay, very firm, massive, may be mottled with light gray.
45-48 ft	Gray to blue gray or tan clay mottled with blue, very firm, massive.
48-65 ft	Light gray clay, massive, very firm, small concretions of CaCO_3 .
65-80 ft	Brownish gray to tan clay, very firm.
80-105 ft	Light gray clay, massive, very firm, small concretions of CaCO_3 .

Chaparral-bristlegrass community

The soil under the chaparral-bristlegrass community is similar to that of the mesquite area. The topography is generally rolling although slope does not exceed 3% in the areas studied. Surface drainage is somewhat better under the

chaparral community. Both the depths of the surface layer and of the parent material are slightly less under the chaparral, but these differences are not significant at the .05 level.

A typical profile is shown in Figure 2. The following profile is representative of the chaparral area:

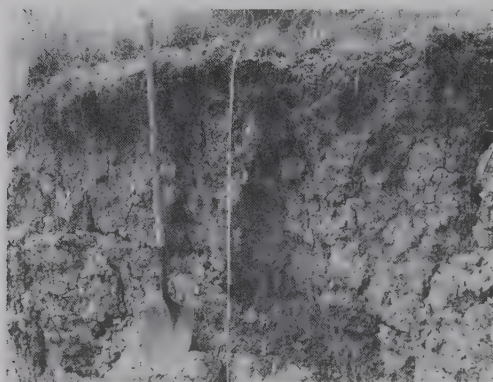


FIG. 2

Depth	<i>Victoria clay</i>
0-18 in.	Very dark gray (10YR 3/1; black 2.5Y 2.0 moist) clay; strong medium granular to weak blocky; very sticky and plastic when wet; large cracks develop upon drying; near neutral to strongly calcareous; 12-26 in. thick.
18-39 in.	Dark gray (10YR 4/1) clay; weak medium blocky, very firm; sticky and plastic when wet; large cracks develop upon drying; calcareous; grades to horizon below; 20-34 in. thick.
39-48 in.	Light brownish gray (2.5Y c/2) clay; strongly calcareous; massive; very firm; transition between weathered top soil and parent material below; 5-12 in. thick.
48 in. plus	Light gray (2.5Y 7/2) clay; strongly calcareous; massive; very firm; contains small concretions of CaCO_3 and occasionally small gypsum crystals; may continue many feet deep.
4-40 ft	Light tan clay mottled with grayish brown, massive, very firm, continuing many feet without change.
40-44 ft	Light gray clay, massive, very firm, grading into layer below.
44-50 ft	Light gray sandy clay, massive, very firm, much more sandy than the layers above or below.
50-75 ft	Light grayish brown clay, massive, very firm, similar to clay layers above.
75-105 ft	Blue gray clay interspersed with small layers of sand. A layer of pale brown fine sand about 2 ft deep usually occurs between 75 and 90 ft.

Few differences were noted between the soil profiles underneath the mesquite-buffalo grass and the chaparral-bristleglass communities. How-

ever, differences in the surface 3-40 ft were found for other communities studied.

Bunchgrass-annual forb community

The bunchgrass-annual forb community was characterized by a thick layer of fine sand over heavy clay material similar to that described above. The sand mantle varied from 3-30 ft in depth. No gravels, mollusk shells or other evidence of water deposition were observed; thus it was assumed that the sand deposits were of eolian origin. A typical profile is described below:

Depth	<i>Nueces fine sand</i>
0-18 in.	Light brownish gray (10YR 6/2, grayish brown 10YR 5/2 moist) fine sand; near neutral; grades into layer below.
18-36 in.	Very pale brown (10YR 7/3) fine sand; loose; near neutral; grades into horizon below.
36-48 in.	Very pale brown (10YR 8/3) fine sand; loose; resting upon a clay base of brown clay mottled with reddish yellow (5YR 7/6 clay); the clay layer occurring between 3 and 30 ft in depth and not always found above 48 in.
4-12 ft	Very pale brown fine sand, loose, grading from darker to lighter with depth, resting upon a clay layer.
12-44 ft	Pale brown clay mottled with red and reddish yellow. This layer may be only a few feet thick or may continue for several feet.
44-68 ft	Very pale brown to light gray sand, extremely fine, similar to sand of the surface layer.
68-94 ft	Light gray clay, massive, very firm, apparently the same clay as found at similar depths under other soils of the area.
94-105 ft	Blue gray clay interspersed with layers of fine sand.

Prickly pear-short grass community

The prickly pear-short grass community was characterized by the dark gray clay loam soils, generally covered with a fine surface layer of light colored sand. The physical condition of the surface layer is generally poor. Little or no cracking was noted during dry periods. A typical profile is described below:

Depth	<i>Orelia clay loam</i>
0-17 in.	Very dark gray (2.5Y 2/0 moist) clay loam; massive; plastic when wet; very hard and crusty when dry; about neutral; grades to horizon below.
17-29 in.	Dark grayish brown (2.5Y 4/2) clay; very firm and compact; extremely hard when dry; very slowly permeable; alkaline; grades to horizon below.
29-48 in.	Light gray (2.5Y 7/2) sandy clay; medium blocky; strongly calcareous; grades to parent material below.
4-15 ft	Light gray (2.5Y 7/0) sandy clay; medium

	blocky; strongly calcareous; small concretions and soft lumps of CaCO_3 present.
15-23 ft	Light gray sand, loose, very fine.
23-45 ft	Light tan clay, massive, very firm, apparently the same material as found under adjoining soils.
45-50 ft	Blue and blue gray clay, massive, very firm, coming out of drill in large chunks.
50-55 ft	Light gray clay, massive, very firm, similar to material above except in color.
55-75 ft	Light brownish gray clay, massive, very firm, similar to material above and below.
75-80 ft	Light gray clay, similar to that above.
80-105 ft	Light gray sandy clay interspersed with thin strata of fine gray sand.

Chemical and physical determinations were not made on material below 42 in. in depth. It was assumed that the chemical properties at lower depths had little effect on the present vegetation.

A combination of surface topography and structure of the underground mass gave some indication of the soil that supported the various plant communities. Using data from the driller's logs, a bisect was mapped of the Lake Pasture at its widest north-south point (Fig. 3).

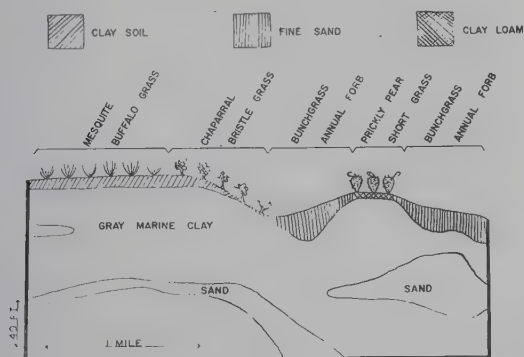


FIG. 3

The topography was level or nearly so from the south boundary of the Refuge to a point about one mile from the boundary. This location also marked the change from the mesquite-buffalo grass community to the chaparral-bristleglass community. The land was gently sloping from the beginning of the chaparral community to the bottom of an escarpment that ran east-west through the study area. The soil of both these communities was a heavy black clay with only minor differences. The clay parent material was apparently the same for both communities. Slope and drainage were the only apparent differences between them.

The bunchgrass-annual forb community began at the base of the escarpment and continued northward for approximately $\frac{1}{2}$ mile. The sand top-

soil was deposited on a clay base similar to that of the other communities. Apparently much of the original clay had been cut away by past erosion. It appeared that all the area from the escarpment to the Aransas River had once been in the stream channel and that the river had shifted its course several times. The resulting depressions had been filled with sand, giving soils distinctly different from those of the surrounding region.

The area containing the prickly pear-short grass community was apparently an island in the clay parent material that extended near the surface. Eolian sand extended on all sides of the island.

Although clay, clay loam, and fine sands all occurred on the same clay base, it is not assumed that this base is the parent material of all the communities listed. Probably the Victoria soils developed from the mass below and the clay layer can be considered the true parent material for these soils. The deep sands are probably of eolian origin, having been deposited in eroded channels by relatively recent winds. The loam soils may have developed from a mixing of the eolian sands with the clay base or may be deposited soils. Therefore, the extensive underground clay deposits should be considered as the parent material of the soils of the mesquite-buffalo grass and chaparral-bristle grass communities only.

Differences between both surface drainage and internal percolation of water were factors in the distribution of the plant communities. The mesquite community was on level clay soil and chaparral on clay soil where drainage was improved. The areas of deep, loose sand had rapid drainage both on the surface and in the soil profile. They supported a grass vegetation essentially devoid of brush. Both surface and internal drainage were good but not excessive in the prickly pear communities.

Physical properties of the soils

Duplicate 3 x 3 in. soil core samples were taken at depths of 0-4 and 6-10 in. at each vegetation sampling location and the percentage of pores at 40 cm water tension and total pore space were determined by the tension table method (Leamer and Shaw 1941). Bulk density measurements for the cores were determined by the procedures outlined by Bayer (1956).

Bulk soil samples were taken with a drainage spade from the sides of the core holes at depths comparable to the cores removed. These samples were used for determining particle size distribu-

tion. The method of Bouyoucus (1936) was employed except that sodium hexametaphosphate was used as a dispersing agent.

Soils under the 4 plant communities ranged from clays to very fine sands. Variations in particle size distribution, bulk density, macro-pores and micro-pores were found between communities. The average values for each of these physical properties are summarized in Table IV.

TABLE IV. Average values for six physical measurements of the soil under four plant communities on the Welder Wildlife Refuge

	Mesquite-buffalo grass community	Chaparral-bristlegass community	Bunchgrass-annual forb community	Prickly pear-short grass community
Sand % (0-6").....	13.28	15.98	87.37	47.65
Silt % (0-6").....	25.80	27.91	9.13	13.18
Clay % (0-6").....	60.64	55.75	3.22	39.17
Bulk density (0-6")...	1.15	1.16	1.44	1.46
Bulk density (6-12")...	1.29	1.29	1.53	1.47
Macro-pores % (0-6")...	11.00	10.62	9.34	8.54
Macro-pores % (6-12")...	7.10	8.31	9.12	7.84
Micro pores % (0-6")...	47.90	46.48	38.79	36.26
Micro-pores % (6-12")...	43.65	43.50	37.02	38.78

Analysis of variance of the physical attributes of the soil revealed highly significant differences between the sand and clay contents of the soils of the 4 plant communities; however, there were no significant differences between the texture of the soil samples taken within communities.

Soils of the mesquite-buffalo grass community and the chaparral-bristlegass communities were similar in texture. Both were well within the clay range, but the mesquite community had soils slightly higher in total clay content and slightly lower in silt and sand. Although slight differences existed in particle size distribution, they were not significant at the .05 level. Soils of both communities were low in bulk density, the surface layer averaging 1.15 and 1.16 g/cc for the mesquite and chaparral communities, respectively. At 6-12 in. depths the mesquite community was slightly higher, averaging 1.39 g/cc to 1.29 g/cc for the chaparral soil.

The soil of the bunchgrass-annual forb community consisted almost entirely of very fine sand. Textural analyses showed this type had an average sand content of 87.37%. No particles were larger than about 1 mm in diameter. Both silt and clay fractions were low. Bulk density values averaged 1.44 g/cc for the surface 6 in. and 1.53 g/cc for the 6-12 in. depths.

Individual samples from the prickly pear community clustered around the dividing line between clay loam, clay, and sandy clay on the

textural triangle. The parent material below was a heavy sandy clay. Bulk density values for the prickly pear community were higher than the clay soils and about the same as the sandy soil. Average bulk density values were 1.46 and 1.47 respectively for the surface and 6-12 in. depth.

Pore volume relationships varied between soils of the 4 communities. Analysis of variance showed that the non-capillary pore space was not significantly different between the 4 communities. Capillary pore space, however, was significantly different at the .05 level. Distribution of capillary and non-capillary pores in the soil of each community had between 55 and 60% total pore space in the upper 6 in. and slightly less than 50% in the 6-12 in. zone. However, non-capillary pore space was low in soils of both communities, and contributed only about 10% of the total volume sampled. Non-capillary porosity was greater in the surface 6 in. under these 2 communities, while capillary porosity changed but little in the surface foot.

Total pore space in the soil of the bunchgrass-annual forb community was generally less than 50%. This was partly responsible for the high bulk density figure reported above. Ratio of capillary to non-capillary pores was relatively constant throughout the surface foot. Little or no aggregation was possible with the extremely low clay content of the fine sand and the soil was essentially structureless with few large pores. However, due to the high sand content and virtual absence of clay, water infiltration was rapid and percolation occurred freely through the soil profile.

The soil of the prickly pear community had high bulk density and a large per cent of soil in relation to pore space. Pore space was relatively constant throughout the surface foot. Non-capillary pores made up only about 8% of the soil volume. Water infiltration was low under the prickly pear community. The surface soil was somewhat dispersed and tended to seal off the water and prevent its entering the soil.

Chemical properties of the soils

A composite soil sample from each of 20 vegetational transect locations in each community was chemically analyzed. Five cores were taken with a Veilmeyer tube immediately along each line to a depth of 4 ft. Six inch sections of each core were combined to make composite samples from 0-6 in., 18-24 in. and 36-42 in., respectively. Soil reaction was measured electrically by a Beckman Model G pH meter. Conductivity, as a measure of total salts, was determined by electrical re-

TABLE V. Average values for chemical analyses of the soils at 20 locations on each of four range plant communities on the Welder Wildlife Refuge¹

	pH ² Range	P ³ PPM	K ³ PPM	Ca ³ PPM	Cl ⁴ PPM	SO ⁴ PPM	Salts ⁵	Organic ⁶ matter
Mesquite-buffalo grass community								
0-6 inches	7.7-8.0	6.9	447	19525	316	68	400	1.46
18-24 inches	7.7-8.1	6.5	497	18424	353	36	590	.93
36-42 inches	7.7-8.1	10.0	718	23075	1008	128	1210	.73
Chaparral-bristlegrass community								
0-6 inches	7.0-8.0	4.5	375	14600	468	56	520	1.73
18-24 inches	7.7-8.2	4.8	424	17700	615	51	750	1.13
36-42 inches	7.3-8.0	8.8	521	21025	1287	756	1630	.75
Bunchgrass-annual forb community								
0-6 inches	6.7-7.5	5.5	113	459	117	24	40	.81
18-24 inches	6.9-7.6	2.5	91	448	101	41	20	.55
36-42 inches	6.9-8.1	3.3	98	535	140	46	10	.33
Prickly pear-short grass community								
0-6 inches	7.1-8.4	5.2	352	10600	92	30	270	2.14
18-24 inches	7.7-8.3	2.9	502	31175	643	37	710	.99
36-42 inches	7.7-8.4	16.4	624	36575	1034	63	950	.65

¹ Analyses determined by Edwina Beckman, Soil Testing Laboratory, The Agricultural and Mechanical College of Texas.² Readings made from a 1:1 water extract on a Beckman Model G pH meter.³ Determinations made from an ammonium acetate extract buffered to a pH of 4.2.⁴ Determinations made from a 1 N nitric acid extract.⁵ Determinations made from a 1:2 water extract with an Industrial Instruments Solu-bridge and reported in electrical conductivity 10⁶.⁶ Determined by a modification of the Walkley-Black method and reported in per cent.

sistance methods using an Industrial Instruments Solu-bridge. Available phosphorus, potassium, calcium and sodium were determined from an ammonium acetate extract by a Beckman flame photometer similar to the one described by Gilbert *et al.* (1950). Methods and procedures outlined by the Extension Service Soil Testing Laboratory of the Agricultural and Mechanical College of Texas were used.

Chemical properties of the soils of the 4 communities varied between communities and between depths within communities. The average values for the chemical properties studied are in Table V.

Soil reaction of the mesquite-buffalo grass community ranged from 7.7-8.0. Active phosphorus and potassium were low while calcium was high at all depths. The values generally increased with depth, being low in the 0-6 and 18-24 in. levels and moderate to high in the 36-42 in. zone. Organic matter was moderately high in the surface layer and decreased with depth.

The soils of the chaparral-bristlegrass community were similar to those of the mesquite community except that they were slightly lower in phosphorus, potassium, and calcium and slightly higher in organic matter, total salts, chlorides and sulfates. The pH was somewhat wider than that of the mesquite soil, varying between 7.0 and 8.2.

Soil reaction in the bunchgrass-annual forb community ranged from 6.7 to 7.5 in the surface layer and from 6.9 to 8.1 in the lower depths. In general, phosphorus, potassium, total salts and organic matter content decreased with depth,

while calcium, chloride and sulfate levels increased with depth. Available nutrients were low at all depths.

Soils of the prickly pear-short grass community were alkaline, with pH values from 7.1-8.4 in the surface 6 in. and between 7.7 and 8.4 in the lower depths. Phosphorus was very low, potassium low, and calcium high at all depths, and the concentration of each increased with depth. Chlorides were low in the surface layer, moderate at the 18-24 in. level and high at the 36-42 in. depth. Total salts and sulfates were low at all levels, but generally increased with depth. Organic matter was moderately high in the surface 6 in. but low at the other depths.

The most noticeable differences between the soil of the prickly pear community and the others were the very high concentrations of calcium and chlorides at the 36-42 in. level under the prickly pear community. Also, the soils of the prickly pear community were lower at the shallow depths in potassium, calcium, sodium, chlorides and sulfates than those of the Victoria series.

Differences of major chemical factors were tested by analysis of variance to determine statistically the extent of the variation. Organic matter content was significantly different between communities and between depths within communities. A highly significant difference existed in phosphorus content between communities and between locations within communities. The soils of the various communities were different at the .01 level in potassium content. Highly significant differences existed in potassium content

between depths, but no significant differences occurred between locations within each community.

Soil moisture relationships

Permanent wilting percentages of the soils of each community were determined by the method of Briggs and Shantz (1912). A plant that normally occurred on all soils, *Croton capitata*, was used as a test plant instead of the dwarf sunflower used by Briggs and Shantz. Twenty core samples, each 3 x 3 in., were taken from the soils of each plant community approximately 24 hrs after a heavy rain and the per cent moisture was determined gravimetrically. The average per cent moisture remaining in the soil was considered to be the field capacity of the soil. A summary of field capacities and permanent wilting percentages is in Table VI.

TABLE VI. Field capacity and permanent wilting percentages in the soils of four range plant communities on the Welder Wildlife Refuge

Community	FIELD CAPACITY		PERMANENT WILTING PERCENTAGE	
	Average	Range	Average	Range
Mesquite-buffalograss..	41.38	(32.0-49.9)	12.27	(11.76-18.05)
Chaparral-bristleggrass..	41.38	(31.7-57.2)	13.46	(13.10-19.08)
Bunchgrass-annual forb.	11.00	(9.6-13.5)	.83	(0.75- 0.90)
Prickly pear-short grass.	32.10	(30.2-33.5)	5.38	(4.50- 6.06)

Field capacities and permanent wilting percentages were not significantly different between the mesquite-buffalo grass soil and the soil of the chaparral-bristleggrass community. However, these communities were different from others studied.

Moisture holding capacity of the clay soils, as reflected by field capacity measurements, was much greater than that of the clay loam or sandy soils. However, the available moisture, or that held between field capacity and the permanent wilting percentage, was not significantly different between the clay and clay loam soils. The fine sand was far below the soils of the other 3 communities in moisture holding capacity. Available moisture held by the 4 communities, expressed as a percentage of the dry weight of the soil, was 29.11%, 28.42%, 10.17% and 26.72% for the mesquite, chaparral, bunchgrass and prickly pear communities, respectively.

Infiltration rates

Water infiltration rates were studied on bare soil, grass sod and brush cover in each community. The concentric ring method described by Leithead (1950) was used.

Infiltration rates varied between communities and between conditions within a community. In general, infiltration was lowest through bare soil, and highest under grass sod.

All vegetation improved water intake on the soil of the mesquite type, but grass proved superior to brush. Under grass sod 8.9 in. of water entered the ground in 2 hrs as compared with 7.5 in. under mesquite and 3.5 in. under bare soil.

The most striking example of grass sod improving infiltration was demonstrated in the chaparral-bristleggrass community where 15 in. with only 2.19 in. under blackbrush and 1.12 in. under bare soil.

The soil of the bunchgrass community was very freely permeable. After 2 hrs, it continued to receive water at the rate of 12.4 in./hr. During the 2 hr period, 30.0 in. entered the soil under vegetation and bare soil infiltrated 23.3 in.

Water infiltration was extremely low under all vegetational conditions on the prickly pear-short grass community. All tests showed less than 2 in. infiltrated in 2 hrs, 1.81 in. entering under prickly pear, 1.47 in. under bare soil and only .76 in. under grass sod. The surface soil was in extremely poor physical condition; this is borne out by the high bulk density and low pore space. Small particles on the soil surface ran together and formed a sealing film that prohibited the intake of water. Vegetation did not greatly increase infiltration rates. Stands of curly mesquite grass actually decreased the amount of water taken.

RELATIONSHIPS BETWEEN VEGETATION AND SOIL PROPERTIES

Many assumptions have been made regarding causes of vegetational distributions on rangelands, but too often data are not sufficiently complete to allow for accurate appraisal of the factors involved. Greig-Smith (1957) stated that the most accurate method of measuring relationships between plants and their environment was to test quantitative data on both plant and environmental factors with correlation coefficients.

Quantitative data were obtained for both plant and soil attributes which could be related mathematically and correlations were calculated between all plant and soil characteristics studied within each plant community.

In general, the smallest amounts of brush cover grew on soils highest in potassium. Total grass cover was generally most dense in areas within communities that were highest in sand or silt. Highest percentages of climax grasses were usually associated with high contents of phos-

phorus and potassium but were negatively related to salt and chloride content. Forb density did not follow a definite pattern throughout all communities, but reacted differently in each vegetational type and did not lend itself to statistical interpretation.

Mesquite-buffalo grass community

Grass cover in the mesquite-buffalo grass community was positively correlated at the .05 level with sand content of the soil (Table VII).

TABLE VII. Correlation coefficients between soil properties and vegetational attributes on the mesquite-buffalo grass community of the Welder Wildlife Refuge

	Grass cover	Brush cover	Mesquite cover	Per cent climax plants	Brush/acre ²
0-6 inches					
Organic matter..	.175	-.131	-.144	-.318	.209
Phosphorus.....	-.099	-.152	-.100	-.442*	-.028
Potassium.....	.134	-.200	-.235	-.082	-.450*
Soluble salts.....	.397	.064	.046	-.050	-.089
Chlorides.....	-.179	.155	.147	-.380	-.390
Sulfates.....	-.122	.297	.281	-.189	.315
Sand %.....	.468*	-.009	-.074	-.530*	-.032
Silt %.....	.084	-.182	-.172	-.226	.127
Clay %.....	-.314	.103	.141	.458*	-.037
Bulk density.....	.027	-.258	-.283	.064	.124
Large pores.....	.212	-.162	-.198	-.220	-.063
Small pores.....	-.268	.003	.019	.269	-.373
18-42 inches					
Organic matter..	-.015	.456*	.416	.138	.405
Phosphorus.....	-.296	-.063	.048	.167	-.133
Potassium.....	.262	.089	.101	.215	.010
Soluble salts.....	-.358	.419	.521*	.378	.387
Chlorides.....	.075	.177	.100	.578**	.031
Sulfates.....	-.056	-.015	-.127	-.113	-.148
36-42 inches					
Organic matter..	.457*	-.362	-.495*	.248	-.019
Phosphorus.....	.069	-.340	-.291	-.176	-.134
Potassium.....	.063	-.484*	-.441*	.677**	.167
Soluble salts.....	-.431	.206	.256	.587**	.550**
Chlorides.....	-.423	.251	.305	.593**	.417
Sulfates.....	-.179	-.124	-.136	.215	-.229

* r values greater than .433 are significant at the .05 level.

** r values greater than .549 are significant at the .01 level.

However, the percentage of climax grasses exhibited a significant negative correlation with sand content. Field data revealed that locations highest in sand content usually supported curly mesquite and buffalo grass, both of which were considered increasers or less desirable for the site. As the clay content of the surface soil increased, more desirable grasses were found. Desirable grasses were most abundant in sampling locations highest in phosphorus (significant at the .05 level). The comparably low phosphorus content and the positive relationship between climax plants and phosphorus content of the soil indicate that the lack of phosphorus may limit the distribution of some of the more important forage producing grasses.

No significant correlations were demonstrated between properties of the surface soil and either mesquite cover or total brush cover. However, the number of brush plants per acre was negatively related at the .05 level to potassium content of the surface soil. Total brush cover and mesquite cover likewise showed a negative relationship with potassium content of the surface soil, but these relationships were not significant at the .05 level. Grass cover and per cent of climax plants were positively related to the amount of potassium in the soil. Although these relationships were not mathematically significant, the general trend appeared to be for increased amounts of brush in areas lowest in potassium content. The inverse relationship between potassium content of the soil and brush density could be due to increased competition from grasses in areas high in potassium and decreased competition from grasses in areas low in potassium.

Climax plants and grass cover declined with increased chloride content of the surface soil, but these relationships were not statistically significant. The areas highest in chloride content supported halophytic forbs which appeared to be more chloride tolerant than did the grass plants. Likewise, the most dense stands of brush occurred where soils of the lower levels were highest in soluble salts and brush appeared to tolerate higher salt and chloride contents than grass plants.

The highest percentages of climax grasses occurred on soils with the highest chloride content at the lower levels. In areas where chlorides in the soil had been leached to a depth below 18 in. grass plants replaced forbs. Also, larger amounts of mesquite were present in locations highest in chloride content at the lower levels, indicating that both forbs and mesquite can tolerate higher chloride contents than grasses.

Organic matter content of the soil and grass density were positively related at the .05 level in the 36-42 in. stratum. In areas where grasses were most dense their deep, fibrous roots extended abundantly into the soil profile thereby increasing the organic matter content at the lower level. A complete summary of correlations between vegetational and edaphic factors in the mesquite community is in Table VII.

Chaparral-bristleglass community

The relationships between soil properties and vegetation in the chaparral-bristleglass community and the mesquite community were similar in many respects. As in the mesquite community, brush cover and potassium content of the soil were in-

versely related. The average potassium content in the soil of the chaparral community was significantly lower than that in the mesquite community and total brush cover for the chaparral community was higher than the average values for the mesquite community, substantiating the inverse relationship between potassium content of the soil and brush cover.

Mesquite cover in the chaparral community was positively correlated at the .05 level with chloride content of the surface soil. High correlations between soluble salts and mesquite cover occurred, but these were not statistically significant. These data further indicated that mesquite is more chloride tolerant than other species present. A summary of the relationships between soil properties and vegetational attributes is in Table VIII.

TABLE VIII. Correlation coefficients between soil properties and vegetation on the chaparral-bristlegrass community on the Welder Wildlife Refuge

	Grass cover	Brush cover	Mesquite cover	Per cent climax plants	Brush/acre ^a
0-6 inches					
Organic matter...	.004	-.210	-.122	-.050	-.108
Phosphorus.....	.319	-.040	-.063	-.003	-.321
Potassium.....	-.374	.019	.299	-.031	-.038
Soluble salts.....	-.125	.194	.412	.323	.038
Chlorides.....	-.005	.256	.539*	-.309	.342
Sulfates.....	.230	.037	.157	-.250	.290
Sand %.....	.067	.372	-.032	.319	.094
Silt %.....	.453*	.063	-.163	-.194	.381
Clay %.....	-.320	-.201	.119	-.030	-.224
Bulk density.....	.176	.160	-.225	.103	.416
Large pores.....	-.530*	.259	.380	.420	-.252
Small pores.....	.346	-.186	-.178	-.428	-.112
18-24 inches					
Organic matter...	-.292	-.142	-.057	-.345	-.046
Phosphorus.....	-.299	.531*	-.102	.323	.093
Potassium.....	-.186	.328	.771**	-.074	.247
Soluble salts.....	.231	-.099	.223	-.311	.329
Chlorides.....	.364	-.270	.030	-.104	.380
Sulfates.....	.217	-.245	-.113	-.035	.325
36-42 inches					
Organic matter...	-.014	.050	.143	.170	-.155
Phosphorus.....	.152	.073	-.114	.074	-.342
Potassium.....	-.092	-.438*	-.164	.084	-.205
Soluble salts.....	.167	.230	-.024	-.093	-.025
Chlorides.....	-.160	-.157	.036	.293	.196
Sulfates.....	.080	.023	-.125	-.274	.401

* r values greater than .433 are significant at the .05 level.
** r values greater than .549 are significant at the .01 level.

Bunchgrass-annual forb community

Few significant relationships occurred between the chemical properties in the surface layer of Nueces fine sand and the vegetational attributes of the bunchgrass-annual forb community. At lower depths per cent climax vegetation was negatively related at the .01 level to sulfates in the soil. Grasses of the Panicoid line grew more abundantly on the soils low in sulfates while in-

vaders of the Eragrostoid-Chloroid line were more frequent on soils high in sulfates.

Although fewer significant relationships existed between chemical properties of the soil and vegetation than occurred in the other communities studied, soil texture was more closely related to vegetation in the bunchgrass community than in the other vegetational types. As the clay content increased in the sandy soil, both grass density and per cent of climax grasses decreased at a highly significant rate. Also, per cent of climax plants was positively related to the sand content of the soil. Clay content was uniformly low in all samples from the bunchgrass-annual forb community and little variance was noted between locations. *Andropogon scoparius* var. *littoralis* was the most abundant climax decreaser on the site and its creeping rhizomes extended more readily in loose sandy soil. Table IX contains a summary of these correlations.

TABLE IX. Correlation coefficients between soil properties and vegetation on the bunchgrass-annual forb community of the Welder Wildlife Refuge

	Grass cover	Range score
0-6 inches		
Organic matter.....	-.202	-.089
Phosphorus.....	-.252	-.272
Potassium.....	-.289	-.016
Soluble salts.....	.248	.118
Chlorides.....	.020	.043
Sulfates.....	-.433	-.330
Sand %.....	.399	.596**
Silt %.....	.282	.477*
Clay %.....	-.512**	-.659**
Bulk density.....	-.195	-.292
Large pores.....	.271	-.009
Small pores.....	.010	-.003
18-24 inches		
Organic matter.....	.148	.407
Phosphorus.....	-.019	-.063
Potassium.....	-.301	-.250
Soluble salts.....	.011	.084
Chlorides.....	-.020	-.034
Sulfates.....	-.034	-.573**
36-42 inches		
Organic matter.....	-.104	.126
Phosphorus.....	.019	-.084
Potassium.....	-.116	-.087
Soluble salts.....	-.089	-.180
Chlorides.....	-.314	-.271
Sulfates.....	-.007	-.235

* r values greater than .433 are significant at the .05 level.
** r values greater than .549 are significant at the .01 level.

Prickly pear-short grass community

Plant-soil relationships within the prickly pear-short grass community were different from the associations studied in other communities. Grass cover in the prickly pear community was negatively correlated with phosphorus content of the soil. Possibly curly mesquite grass and sand burs

which did not occur in large amounts in the other communities did not have such requirements for phosphorus as did the grasses there.

Organic matter content of the soil at lower levels and grass cover were positively related at the .05 level, indicating that the deep roots of the grass plants increased the organic matter content of the soil.

Total brush cover was positively correlated with sulfate content of the soil at the 36-42 in. depth. However, since the two were not related in the surface soil and negatively related at the 18-24 in. depth, little significance could be attributed to the mathematical relationship.

Mesquite cover exhibited a negative association with both organic matter content of the soil and micro-pore space in the soil. This association probably reflects the decreased amounts of grass in the areas heavily infested with mesquite. As in the other communities, brush density was positively correlated with both soluble salts and chloride content of the soil. A summary of the correlations is in Table X.

TABLE X. Correlation coefficients between soil properties and vegetation on the prickly pear-short grass community on the Welder Wildlife Refuge

	Grass cover	Brush cover	Mesquite cover	Percent climax plants	Brush/acre ²
0-6 inches					
Organic matter...	-.137	.048	.004	.134	-.259
Phosphorus.....	-.434*	.411	.400	.287	.081
Potassium.....	.030	-.355	-.104	-.152	-.348
Soluble salts.....	-.284	.091	.184	.343	.378
Chlorides.....	-.061	-.263	-.086	-.306	.032
Sulfates.....	-.196	.049	-.032	.132	.010
Sand %.....	-.199	.133	.307	.089	.048
Silt %.....	.402	-.278	-.214	-.295	-.056
Clay %.....	-.017	.017	-.218	.076	-.020
Bulk density.....	-.024	-.164	-.279	.104	.429
Large pores.....	.024	.503*	.001	.299	.125
Small pores.....	.050	-.356	-.183	-.397	.647**
18-24 inches					
Organic matter...	.143	-.525*	-.434*	-.079	-.339
Phosphorus.....	-.057	-.223	-.149	.023	.398
Potassium.....	-.149	.233	.157	.007	-.244
Soluble salts.....	-.123	-.295	-.234	.322	.536*
Chlorides.....	-.066	-.214	-.220	.215	.533*
Sulfates.....	-.223	-.285	-.363	.460*	.095
36-42 inches					
Organic matter...	.441*	.044	-.395	-.040	-.113
Phosphorus.....	-.557	.058	.652**	.111	-.030
Potassium.....	.156	.134	-.334	.111	-.154
Soluble salts.....	-.056	-.119	.064	.325	.001
Chlorides.....	-.148	.064	.341	-.011	.248
Sulfates.....	-.188	.472*	.308	.395	-.177

* r values greater than .433 are significant at the .05 level.

** r values greater than .549 are significant at the .01 level.

DISCUSSION

Large areas of brush occur in the Texas Coastal Prairie, yet the region was described as open grassland less than a century ago (Havard 1885).

In areas that are apparently similar in climate and land use, several recognizable brush communities may grow in close approximation to one another. The breaks or transitional zones between communities usually follow observable changes in soil, indicating that local edaphic factors and plant communities are closely associated.

Within the 3968 acre area of the Lake Pasture of the Welder Wildlife Refuge are 4 distinct plant communities. The land had been used for commercial cattle production for over 100 yrs, and probably had never been sub-divided into smaller pastures. Since the entire area was subjected to approximately the same land use and had a relatively uniform climate, it offered nearly ideal conditions for the study of plant community relationships.

Diversity of brush cover was one of the most noticeable differences in the floristic composition between the 4 communities. Mesquite made up more than 95% of the total brush cover in the mesquite community, while on the chaparral community it comprised only a small portion of the canopy. Prickly pear was virtually absent from the mesquite, chaparral and bunchgrass communities, but covered almost $\frac{1}{4}$ of the area in the prickly pear-short grass community.

Few annual forbs and grasses that occurred on the other communities were found on the bunchgrass community. Such plants as balsam grass, seacoast bluestem, knotroot panic, bull nettle and rough leaf nama were only in the bunchgrass community and were excellent indicator species for the deep sandy soil.

Floristic composition of the herbaceous vegetation varied little between the mesquite and chaparral communities. The same species occurred on both soils, but they differed in their per cent composition and relative abundance. Brush stands predominantly of chaparral usually grew on soils with good surface drainage and free percolation capacities. Dense stands of running mesquite usually were associated with extremely fine textured soils with slowly permeable and poorly aerated profiles.

The prickly pear community was comprised of species from both the deep sandy site of the bunchgrass community and from the fine textured upland site of the mesquite and chaparral communities. Combinations of mesquite, chaparral, buffalo grass, curly mesquite grass and plains bristlegass from the clay sites and sand burs, hooded windmill grass and skunk daisy from the deep sandy site typified the area. Prickly pear was not confined to the area, but was not abundant elsewhere.

Not only were there observable differences in the floristic and vegetational properties of the plant communities, but their associated soils varied in color, texture and structure. In addition to the observable differences, statistically significant variations between many chemical and physical properties were demonstrated.

Data from analyses of the properties of the soil and observations from seismograph drillings over the area suggested that only the soils of the mesquite and chaparral communities were genetically related. These appeared to have developed from the same parent material of a fine textured, gray, marine clay and differed from each other only in minor characteristics. The soils of the chaparral community probably developed under slightly different relief, the slope being somewhat steeper than that of the mesquite community. The diverse vegetation of the 2 communities probably has also contributed to the soil differences. These are great enough to support different combinations of brush species, but not large enough to greatly affect the potential production of the 2 communities.

The soil of the prickly pear community developed from a heavy sandy clay that occurred in thick layers over the base of marine clay; that of the bunchgrass community developed from deep depositions of eolian sand. These soils were unlike one another and different from the soils of the other 2 communities.

Range technicians generally classify the area containing the 4 plant communities into 2 range sites. The mesquite-buffalo grass, chaparral-bristleglass and prickly pear-short grass communities are included in a "hardland site" while the bunchgrass-annual forb community is placed in a "sandyland site." Data from this study revealed statistically significant differences in plant species, grass cover, brush cover, mesquite cover, forb density, brush density and litter deposited between the 4 communities. Distinguishable differences were demonstrated between texture, porosity and bulk density values of the soils of the communities. Significant dissimilarities existed between chemical soil properties of the 4 communities. Only small differences existed between the soils of the mesquite and chaparral communities, but large differences occurred between these communities and those of the prickly pear and bunchgrass communities.

Although vegetational and edaphic variations between communities were sufficiently large to warrant the division of the study area into 4 separate sites, this fine distinction probably would not be justifiable for practical management of

the rangelands. However, the large differences between vegetational composition, production and seasonal aspect appeared large enough to justify division of the area into at least 3 major sites.

In general, the areas of Victoria and Monteola clay should be considered one site and areas of Orelia clay and clay loam should comprise another. The deep sands of the Nueces series, which supported the bunchgrass-annual forb community, were significantly different from the others studied and should be considered separately.

Production of forage among the bunchgrass, mesquite and chaparral communities was about equal, but in the prickly pear community it was decidedly lower (Box 1960). Phenology of forage plants was earlier on the sandy soil of the bunchgrass-annual forb community than on the other sites.

Vegetational analyses and statistical calculations from plant and soil properties of the 4 communities suggest that they are distinct ecological entities. Separate problems are incurred in the management of each, and each site should be considered separately in a land use program.

Fairly consistent relationships between soil and plant properties throughout the communities allow generalizations to be made with some accuracy. The greatest amount of mesquite cover was found on soils high in clay content, substantiating the data of Huss (1959). The largest number of mesquite plants per unit area, however, grew on the clay loam sites. Contrary to the findings of Huss, the most dense canopy cover of chaparral species occurred in soils with sand contents of 30% or less. Neither brush nor prickly pear occurred in abundance on soils with sand contents greater than 85% and cactus was rare in soils with clay contents higher than 55%.

Huss (1959) suggested a relationship between gypsum content of the soil and presence of running mesquite. This was not evident in this study. The soil of the mesquite community was low in sulfates. Although no direct tests were made for gypsum, the low sulfate content appeared to rule out the possibility of large amounts of gypsum in the soil. Also, no correlation was found between running mesquite and sulfate content in the soil of any community.

Grass density was not uniformly related to any particular chemical or physical property of the soil, although some significant correlations were found in most communities. Increased percentage of climax grasses were usually associated with increased phosphorus and potassium contents of the soil. Phosphorus was extremely low in the soils

of all communities and more climax grasses were present in areas with high phosphorus content.

Brush cover was inversely related to potassium content in the soil. This relationship was demonstrated by negative correlations between potassium and brush canopy in all communities where brush occurred. The mesquite-buffalo grass community had the highest average potassium content, followed by the prickly pear and chaparral communities, respectively.

Some differences in soil physical properties appeared to be associated with vegetation. Bulk density values decreased where large amounts of litter were incorporated into the soil, and non-capillary porosity increased under similar conditions. Improved physical structure was related to deep rooted grasses that were decreasers for the area. Dense stands of annual vegetation resulted in increased bulk density and reduced pore space.

Water infiltration rates were improved by vegetation on all soil types. In general, grass sod was the best cover for allowing water to enter the soil. This was particularly true in areas where good stands of perennial grass grew and litter was present on the soil surface. Cover of blackbrush, mesquite and prickly pear increased infiltration rates over bare soil, but the associated increase was due to the accumulation of litter underneath the plants rather than to improved structure of the soil. Dead leaves and twigs prevented the soil surface from sealing and continued to allow water to enter the ground. Inspection of profiles under brush and prickly pear cover revealed that only the surface few inches exhibited characteristics associated with good structure. However, those of profiles examined under grass sod were well granulated and aerated for more than 2 ft below the surface.

SUMMARY AND CONCLUSIONS

Soil and vegetational properties associated with mesquite-buffalo grass, chaparral-bristlegass, bunchgrass-annual forb and prickly pear-short grass communities were studied on the Welder Wildlife Refuge in southern Texas. Intensive field and laboratory investigations during 1957, 1958 and 1959 revealed the following:

1. The 4 plant communities were different in measurable characteristics of floristic composition, plant density, cover, frequency and abundance. The mesquite and chaparral communities supported the same species but differed in frequency and relative abundance of the plants. The bunchgrass-annual forb community contained many endemic species and few taxa that occurred on

other communities. Woody plants of the prickly pear community were largely the same as those of the others, but many succulents and forbs were somewhat restricted to the area.

2. The soils of the mesquite and chaparral communities were heavy clays with low bulk density, moderate non-capillary porosity and high capillary porosity. The soil of the bunchgrass community was a very fine sand with relatively high bulk density and moderate porosity. The clay loam of the prickly pear community was high in bulk density and low in pore space.

3. Phosphorus, potassium, soluble salt and organic matter content of the soil varied among the communities. Clay and clay loam soils of the mesquite, chaparral and prickly pear communities were relatively high in fertility and that of the bunchgrass community comparatively low.

4. The 4 plant communities occurred on 3 soil types. The mesquite and chaparral communities occurred on Victoria clay, the prickly pear community on Orelia clay loam and the bunchgrass community on Nueces fine sand. The soils of the mesquite and chaparral communities developed from similar parent material of gray, marine clay. Soils of the other 2 communities have been deposited on the clay base at a later time.

5. Water infiltration rates of the soil profiles were significantly different between communities. Soils in the chaparral and mesquite communities were high in moisture holding capacity but low in permeability. The fine sands of the bunchgrass community were very highly permeable. Moisture retention was moderate but water infiltration and percolation were extremely low in the soil of the prickly pear community.

6. The differences in edaphic and vegetational properties of the communities were sufficiently great to justify dividing the area into 3 range sites. The mesquite and chaparral communities occurred on an upland fine textured site, the prickly pear community on an upland mixed soil site and the bunchgrass community on a deep sandy site.

7. Forage production between communities was about equal with the exception of the prickly pear community which was significantly lower than the others. This lowered production was associated with the poor physical conditions of the soil and undesirable water relationships in the community.

8. Differences in brush cover were negatively related to potassium content on all soils where brush occurred. Brush was not found on soils with sand contents greater than 85%.

9. Brush composition was associated with topography and drainage in the soil. Mesquite was most abundant in the poorly drained areas, while chaparral comprised the largest percentages of total brush cover on clay soils with slopes greater than 2%. Mesquite was also associated with low soil porosity.

10. Vegetation on the soil improved water infiltration rates on all sites. In general, the greater amount of infiltration occurred in soils covered with grass sod followed by soil covered with brush and bare soil. One exception was observed in the prickly pear community, where the presence of curly mesquite grass gave lower infiltration rates than occurred on bare soil.

11. Presence of brush was associated with increased litter on the soil surface and was related to reduced soil porosity and increased bulk density values of the soil. Occasionally, a combination of increased brush density with ungrazed grasses growing beneath the woody plants resulted in increased porosity in the upper few inches.

12. Largest percentages of climax grasses were in locations where the soil contained the highest content of phosphorus. High percentages of climax grasses were associated with low bulk density values of the soil and high macro-pore space.

13. No consistent relationship was found between soil factors and density of forbs. Presence and abundance of forbs appeared to be associated with disturbance factors and increased utilization rather than with soil factors.

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REPORTS

IDENTIFICATION OF *TRIBOLIUM* SPECIES BY PUPAL CHARACTERISTICS¹

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Two species of flour beetles, *Tribolium confusum* Du Val and *Tribolium castaneum* (Herbst), are widely used as laboratory organisms in the field of population ecology. Today, they are also becoming established in laboratories studying artificial and natural selection.

In such work it is frequently advantageous, if not even mandatory, to distinguish between the species. For the imaginal stage this is readily accomplished by using the eye and antennal characters given in Hinton's key to the species of *Tribolium* (Hinton 1948). However, there is no published account of a technique for distinguishing species in their immature stages. A method is described herewith by which the pupae of *Tribolium confusum* can be differentiated from those of *T. castaneum*.

Figure 1 is drawn as a dorsal view to show 6 tergites of the pupae of each species. Several differences in the

¹ I am indebted to Dr. Kumar Krishma for the illustration.

² While this manuscript was in preparation, Mr. Frank K. Ho published a description of another technique for determining these species in the pupal stage (Annals Ent. Soc. of Amer., Vol. 53, No. 2, pp. 280-281). He relied on comparison of the shapes of the genae and on eye characters which appear at a pupal age of about one day. These criteria are useful corollaries to those described above.

patterns of arrangement and relative lengths of the lateral bristles are immediately apparent, and these differences are consistent from tergite to tergite. The bristles labeled *a*, *b*, and *c* in each drawing are diagnostic. For *T. confusum*, bristle *a* is longest, *b* is intermediate, and *c* is the shortest. For *T. castaneum*, *a* is still longest, *b* is the shortest, and *c* is intermediate. These differences in the relative lengths of the lateral bristles are quite apparent even at magnifications as low as 7 times.

After some practice the species are easily discriminated by observing the length of the first bristle (*a*) which is about twice as long in *T. confusum* as in *T. castaneum*. Other species differences are equally valid but not so easily seen. On the penultimate tergite in *T. castaneum* there is only one long bristle while there are 2 in *T. confusum*. Also, the dorsal aspect of the tergites in *T. castaneum* are more densely pubescent than in the other species.

The accuracy of this method has been attested by its invariable success when used to distinguish between the pupae of the 2 species.

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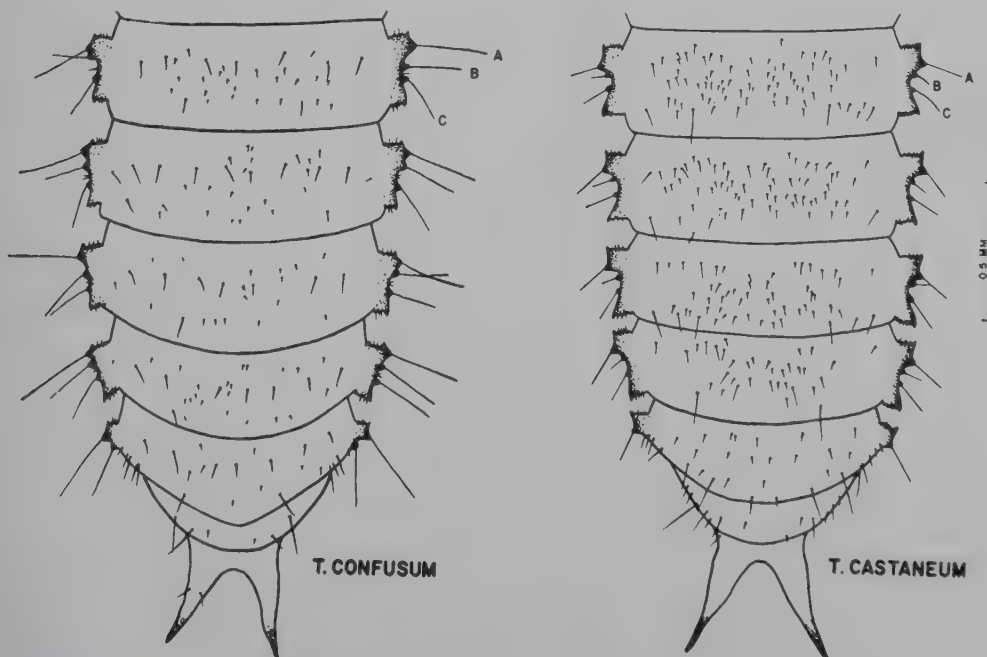


FIG. 1. A dorsal view of the posterior 6 tergites of the pupae of *Tribolium confusum* Du Val and *Tribolium castaneum* (Herbst) comparing the species diagnostic lateral bristles: *a*, *b*, and *c*.

OVERGRAZING OF ALGAE BY HERBIVOROUS MARINE FISHES¹

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The growth of benthic algae in the intertidal zone in the Hawaiian Islands is usually luxuriant but in deeper regions, where suitable bottom affords attachment, it is often restricted to a low stubble. The paucity of algae is most evident in reef areas in which the available hard surface for plant growth is restricted by the presence of living coral. Since herbivorous animals of a size greater than a few inches do not graze extensively on algae in the intertidal zone (tides in Hawaii are small), the short length of the thalli on rock or reefs which are always submerged may result from heavy grazing by plant-feeding animals.

The dominant herbivores in Hawaiian waters are fishes, especially the surgeonfishes (Acanthuridae) and certain parrotfishes (Scaridae). These groups represent the most abundant fishes of moderate size regardless of food habits. Paradoxically, they are still the most abundant in coralliferous areas (an analysis of the populations of Hawaiian reef fishes by underwater transect has been made by Brock 1954). Other important plant-feeders are the omnivorous damselfishes (Pomacentridae) and various echinoids.

To test the overgrazing hypothesis, 4 enclosures of one-inch mesh wire one square foot in area were attached to coral-free sections of the rocky bottom of coral-rich Kealakekua Bay near Captain Cook's Monument on the island of Hawaii at depths of 4 to 6 feet in April, 1955. The enclosures prevented larger herbivores from feeding on the algae. Prior to being covered, the small areas were observed to be grazed repeatedly by herbivorous fishes, especially the surgeonfishes *Acanthurus leucopareus*, *A. achilles* and *Zebrasoma flavescens*. The surgeonfish *Ctenochaetus strigosus* is at least as common as the above species but it is a detritus feeder and the algae it consumes is mostly already detached from the bottom (Randall 1955). The most abundant acanthurid in inshore waters in Hawaii, *Acanthurus triostegus*, is not common in areas with high coral cover like the experimental site, probably because it is less inclined than other species of *Acanthurus* to crop close to the substratum (Randall, 1961).

A study site on Hawaii was selected because a comparable area on Oahu is more apt to be disturbed by the many skin divers and fishermen at this more populous island.

One month after the enclosures were affixed to the bottom the author was informed by an acquaintance on

Hawaii that the algal growth inside the enclosures was distinctly greater than outside. Two months after the enclosures were put down, the author was able to go to Hawaii to examine them. The algae outside averaged about 1 mm in height with little extending above 2 mm. Within the enclosures the height varied with the species. The dominant alga, *Ectocarpus indicus*, attained a height up to 15 mm; an unidentified species of *Polysiphonia* averaged 4 to 6 mm; *Sphacelaria tribuloides* and *Jania* sp. grew from 3 to 5 mm high; a species of *Cladophora* reached 25 to 30 mm.

Data on grazing by fishes limiting the upward growth of algae have also come from a study of the growth of sea urchins (*Diadema antillarum*) at a depth of 6 ft in Lameshur Bay, St. John, Virgin Islands. A wire enclosure excluded fishes from one square yard of rocky bottom from March 21 to June 7, 1961. During this period 16 of the herbivorous *Diadema* tripled in size. Despite this, the algae within the enclosure grew much more than outside. The dominant species (identified by H. J. Humm) were the red *Spyridia filamentosa* which reached a height of 185 mm, and the brown *Dictyota bartayresii* which grew up to 90 mm; parrotfishes and surgeonfishes immediately began grazing when the enclosure was removed.

Stephenson and Searles (in press, Australian Journal of Marine and Freshwater Research) have studied the grazing of algae by fishes at Heron Island on the Great Barrier Reef of Australia more extensively and have obtained similar results.

Another overgrazing affect on marine plants by herbivorous fishes in tropic seas has been demonstrated. In the West Indies parrotfishes and surgeonfishes are responsible for feeding on sea grasses (*Thalassia testudinum* and *Syringodium filiforme*) next to well-developed reefs to the extent that a band of bare sand of about 20 to 30 feet in width separates inshore reefs from the grass beds (Randall, MS).

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NEAREST NEIGHBOR CONCEPT APPLIED TO POCKET GOPHER POPULATIONS¹

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The distances between neighboring catches of pocket gophers were recorded in a study of territoriality in *Thomomys talpoides* in western Colorado. Pocket gophers (*T. talpoides*) are solitary during the non-breeding season and, in Colorado, live in strongly defended territories from the middle of August until the middle of March (Hansen and Miller 1959). Co-

habitation occurs during the breeding season. Following the breeding season and dispersal of young the territories become established and remain relatively stable and mutually exclusive until the next breeding season.

A record of the sites of capture was kept for 2 successive years for a circular study area on Black Mesa, Gunnison County, Colorado. The study plot was 400 feet in diameter with a 20 foot "buffer strip" around the periphery. At the densities encountered it was impossible

¹ Colorado Experiment Station Technical Journal Article S.S. 685.

to delimit by visual observation the extent of individual burrow systems. The study area was saturated with Macabee gopher traps during September in 1955 and 1956. Approximately 6 traps were set for each pocket gopher and trapping was continued until all of the gophers were caught. The location for each capture was plotted on a map showing the circle and the buffer strip. At the time of trapping there was only one pocket gopher per burrow system as no plural captures were made.

Numbers were assigned to each location where a catch was made and the distances between neighboring catches were measured from the map with dividers. The circular study plot was divided into 4 equal sectors which provided 8 different samples for analysis. The catches in the buffer strip were used only for computing the distances between closest neighbors. Density was determined by counting the numbers of catches within each sector of the circle for each year.

Ninety-one pocket gophers were trapped within the 400 foot circular plot in 1955 and 107 were trapped in 1956 (Table I). There were no significant differences in the overall population density, adult to young ratio, or sex ratio for the 2 years. The population was more evenly distributed within the study area in 1956 than in 1955. The distributions of catches for both years were tested for regular and contagious patterns of displacement (Curtis and McIntosh 1950) and it was found that both approached a random distribution. The tendency toward regular distribution was indicated where densities were highest and a tendency toward contagious distribution at the lowest densities.

TABLE I. Average distance to closest 4 neighbors at known density for pocket gophers

Sector (.72 acre)	Number of animals	Density per acre	Distance Ave. $\pm$ S.E.	Number of animals	Density per acre	Distance Ave. $\pm$ S.E.
1.....	15	20.8	40.0 $\pm$ 2.1	32	44.4	31.6 $\pm$ 0.8
2.....	19	26.4	39.3 $\pm$ 1.5	20	27.8	32.5 $\pm$ 2.4
3.....	18	25.0	42.6 $\pm$ 3.1	29	40.3	30.2 $\pm$ 0.9
4.....	39	52.4	25.3 $\pm$ 1.0	26	36.1	32.2 $\pm$ 1.5

The average distance between catches decreased as density increased. This inverse relation was studied for nearest neighbors. The best correlation was obtained with the average of the 4 nearest neighbors. This correlation averaged overall for individuals captured was .963 using the equation: $Y = ax^b$. This equation is handled as:

$$\text{Log } Y = \text{Log } a + b \text{ Log } x,$$

where

Y = density (gophers/acre),

x = average distance between catches,

a = value of Y when $x=0$; a locates the regression line relative to $Y=0$,

b = the change in Y for a unit change in x .

In the above, b is the change in density for each increment increase in distance between catches. This logarithmic relation seems best suited to the situation, at least within the range of available data for all situations observed.

The average distance to the 4 closest neighbors was used because the measure of distance in this sense includes the idea of an area bounded by 4 points. Distances between neighbors might be considered as an indirect

measure of territory size. Although a prediction of this sort seems feasible, we observed a wide range of variation in average distance between neighbors within small areas.

Since density and average distance to the nearest 4 neighbors provided a high degree of correlation, it was decided to investigate the possibility of predicting density by measuring the distance between catches along a transect. Presumably, the average distance between such catches might be a measure of density and territory if one considers the average distance between catches to be an index to the average length of intercept across the territories of pocket gophers.

A study was made of the distances between catches along eight 300 foot transects in areas where density was later determined. Macabee traps were placed in all gopher runways intercepted along the transect lines. Tunnels were located by pushing a probe into the ground at about 4-inch intervals along the transect line until an open tunnel was found. In this way each burrow system usually contained several traps. The samples were taken at Black Mesa in September 1958, when the territories of individual pocket gophers were established. Most specimens were taken in less than 24 hours, and it was possible to remove all gophers in less than 3 full days.

A square one-acre study area, plus a 20 foot buffer strip, was superimposed upon each of the transects. Traps were placed in this area as soon as all gophers had been removed from the transect, and trapping continued until all the gophers had been removed. Density was estimated by counting all gophers caught within the boundary of the acre.

Density on the 8 transects varied from 22 to 37 per acre and averaged 29 pocket gophers per acre (Table II). Using the equation $Y = ax^b$, a correlation of .246 was observed. The average distance between captures on a transect is an index to the average length of intercept across the territories of pocket gophers, whereas, the average distance of the 4 closest neighbors in "area trapping" is an index to the average diameter of the territories of pocket gophers. The average distance between catches along the transects was less than the average distance to the 4 closest neighbors for a given pocket gopher density. Therefore, the units of measure between neighbors in area trapping and transect trapping are not the same.

TABLE II. Average distance between captures along transects at known density for pocket gophers

Transect (300 ft)	Density per acre	No. captures per 300 ft.	Distance Ave. $\pm$ S.E.
1.....	22	7	42.9 $\pm$ 14.7
2.....	24	9	33.3 $\pm$ 5.8
3.....	26	9	33.3 $\pm$ 3.8
4.....	28	10	30.0 $\pm$ 3.9
5.....	28	9	33.3 $\pm$ 4.5
6.....	30	10	30.0 $\pm$ 3.6
7.....	35	8	37.5 $\pm$ 9.6
8.....	37	9	33.3 $\pm$ 6.7

DISCUSSION

The size of territories in relation to population density has received only minor study. Little is known as to how territories change in response to population fluctuations. Within a population the sizes of territories may

vary in relation to the different requirements of the individuals as well as to the kind of habitat. The data from this study indicate a relationship between territory size and density. The sizes of territories appeared to be most nearly the same at high densities and variability increased as density decreased. At low densities, pocket gophers are clustered together and much vacant land occurs between colonies. At average densities, which could occur only in average to excellent habitat, the sizes of the individual territories appear to approach a normal distribution. However, at high densities, which could only occur under excellent habitat conditions, the sizes of pocket gopher territories appear to be very similar and distributed in a regular pattern.

Accurate methods for estimating pocket gopher population density require a great amount of time and effort (Ingles, Clothier, and Crawford 1949). The use of average distances to closest neighbors may be used to

show density relationships. However, the accuracy of estimates based on the "nearest neighbors" in pocket gophers appears to be proportional to the work involved. Under certain circumstances it may be more feasible to obtain density estimates from trapping transects than by trapping plots.

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RELATION OF SUBSTRATE MOISTURE TO ABSORPTION AND LOSS OF WATER BY THE SALAMANDER, *PLETHODON CINEREUS*

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Amphibians normally do not drink water and regulation of moisture content of the body depends on (1) dermal absorption, (2) evaporative loss through the skin, and if present the lungs, (3) loss through the kidneys, and (4) production of metabolic water. Previous studies on water balance of amphibians have not been concerned with properties of the substrate and their role in moisture economy. Those dealing with water loss have been mostly determinations of vital limits or rates of loss in dry air or on artificial substrates (Hall 1922, Thorson and Svihla 1943, Littleford *et al.* 1947, Cohen 1952, Thorson 1955, Ray 1958). On the other hand, those considering uptake of water have treated semi-aquatic species functioning in an aquatic environment, with absorption taking place from water or from solutions of various sorts. An exception is the study of Cohen (1952) which compared rates of water absorption of some terrestrial salamanders. However, as he was not directly concerned with the effect of substrate properties on absorption, the experimental animals were allowed to hydrate on wet paper towels. Only one of the above authors (Littleford) worked on *Plethodon cinereus*. He found that the vital limit of this species was higher than those of other species from more moist habitats. Heatwole (1961) has shown that the eggs of *P. cinereus* can absorb water from a wet substrate and that the rate is greater in small clutches than in larger ones.

In the present study, naturally occurring substrates are used to relate environmental moisture conditions to water economy of *P. cinereus*, a completely terrestrial salamander. Several new concepts are introduced and defined, including (1) "absorption threshold" which is the level of substrate moisture above which there is a net gain in body water by dehydrated salamanders and below which there is a net loss, (2) "critical level" which is the substrate moisture below which water loss by salamanders increases sharply, and (3) "limiting range"

which is the range of substrate moisture values between the above two points.

Because gravimetric expressions of substrate moisture are determined in part by the specific gravity of the material, determinations of absorption threshold and critical level expressed in this way are of limited value and apply only to particular, often local, situations. In order to permit comparison of *P. cinereus* with other amphibians occurring on different substrates, and because this species itself occupies a broad geographical range and is found on many different soil types, it was desirable to use some other unit. The most suitable one is a statement of the force with which water is held in the soil and therefore of the force necessary to extract it. This has gone by various names but is usually called the soil moisture tension and can be expressed in any unit of force or as a value of pF which is the logarithm of the height in cm of a column of water exerting an equivalent force (Schofield 1935). Either of these units permits direct comparison of different substrates. An added advantage is that absorption threshold or critical level expressed in these terms should be the same for all substrates and thus comparison of the physiological properties of different species of amphibians occurring on different substrates would be permitted.

For determining soil moisture tension, 3 series, each of 5 substrate samples, were analyzed in a pressure membrane extractor (Richards 1941) equipped with a mercury differential regulator, and the pressures applied plotted against the mean values of moisture content expressed in percent dry weight. This gives a curve called a "characteristic curve" (Richards 1949) which can be used for converting gravimetric values to their corresponding expressions of tension (Figures 1 and 2).

The substrates used were Roselawn Sand (Foster *et al.* 1939) taken from oak-pine-aspen forest near the University of Michigan Biological Station, humus (mor

type) from a beech-maple forest at Carp Lake, Michigan and Rifle Peat (Veatch *et al.* 1930) from the Mud Lake Bog research area of the University of Michigan. Salamanders were associated with all but the latter type.

Two experiments were carried out, Experiment I at the University of Michigan Biological Station, and Experiment II at Ann Arbor, Mich. They will be considered separately.

EXPERIMENT I

Materials and method

This experiment was designed to determine the absorption threshold for *Plethodon cinereus*, to demonstrate the relationship between soil moisture and rate of evaporative loss in salamanders, and to provide preliminary observations on the effect of substrate moisture on rate of dermal absorption.

Fifteen cardboard ice-cream carton lids, 8.5 cm in diameter and 1.7 cm deep were filled with humus and an additional 17 with sand. Moisture content of the samples ranged from 0.8% to 37.3% dry wt for sand and 18.7% to 321.0% dry wt for humus.

The salamanders used were red adult males between 0.67 and 1.25 g hydrated weight and had been previously kept for at least one week in a terrarium containing wet, sterile litter, and therefore, each animal had an empty gut and was fully hydrated. At the beginning of the experiment they were placed in dry cardboard boxes and allowed to desiccate for one to 2 hours following which

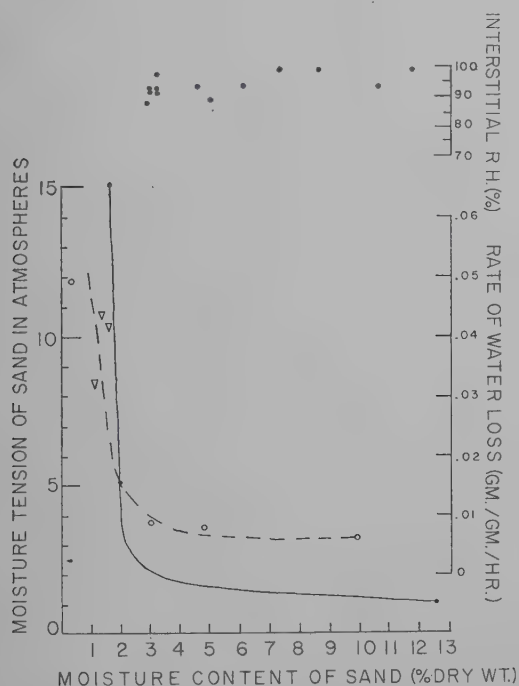


FIG. 1. Characteristic curve for Roselawn Sand and the relation of water loss by *P. cinereus* to moisture content and interstitial relative humidity of sand. Circles represent salamanders which survived the experiment, triangles those which did not. Each point on the characteristic curve represents the mean of 5 values.

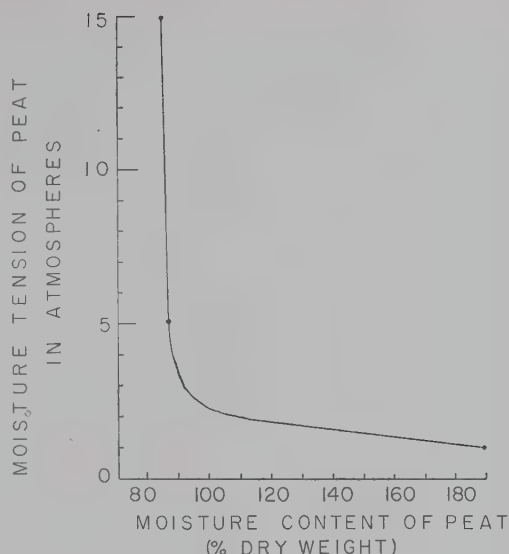


FIG. 2. Characteristic curve for Rifle Peat. Each point on the curve represents the mean of 5 values.

they were placed in separate carton tops. A deep groove was made in the surface of the substrate and a salamander laid in it and covered with material previously taken from the groove. All carton tops were placed between 2 pieces of glass, weighted with stones, and allowed to remain 6 hours at room temperature. There was no gap between substrate and glass and the salamanders were therefore exposed only to relative humidities within, and at equilibrium with, the sand or humus. All salamanders were weighed before and after desiccation and again following their removal from the substrate at termination of the experiment.

Field measurements of the relative humidity in the interstices of the soil were made by the sulfuric acid method of Thamdrup (1939) but with modification of the equipment as described by Heatwole (1959).

Results

The initial desiccation of the salamanders resulted in a water loss of 7.3 to 27.8% of hydrated weight. None died from this treatment, although after the 6-hour experimental period 5 salamanders in the drier substrates were dead. The maximum water loss survived by a salamander in the present experiment was 28.96% of hydrated weight. Littleford *et al.* (1947) gave 25.88% of hydrated weight as the average lethal point for this species.

In sand with a water content of 9.8% or less, all salamanders lost weight whereas those in sand with 11.9% moisture or more gained. Thus, the absorption threshold on sand lies somewhere between. When the gravimetric values are transformed to the corresponding expression of tension by using Fig. 1, the absorption threshold is seen to be between 1 and 1.5 atmospheres or at a pF value of 3-3.2. This value should be a constant regardless of the substrate employed. Unfortunately, when the tension-substrate moisture analyses were made, humus samples from the Carp Lake area were not available and tension values for this substrate were not determined.

On a gravimetric basis, the lowest values of humus moisture at which absorption took place was 76.1% dry wt and the highest value at which the salamanders lost weight was 67.1% dry wt with the absorption threshold falling somewhere between.

The relationship of moisture loss of salamanders to the water content of the substrate was quite definite. On sand which was below the absorption threshold, salamanders lost body water at a gradually increasing rate (from 0.005 to 0.008 g water per g hydrated wt per hr) until sand moisture values of 2.5% (2.5 atm) were encountered (Fig. 1). Below this level, rate of water loss increased markedly, climbing to 0.049 g/g/hr. The same pattern of change in rate occurred on humus (Figure 3). There the increase in rate of loss took place at substrate moisture values of 30-35% dry wt. However, tension units are not available for comparison.

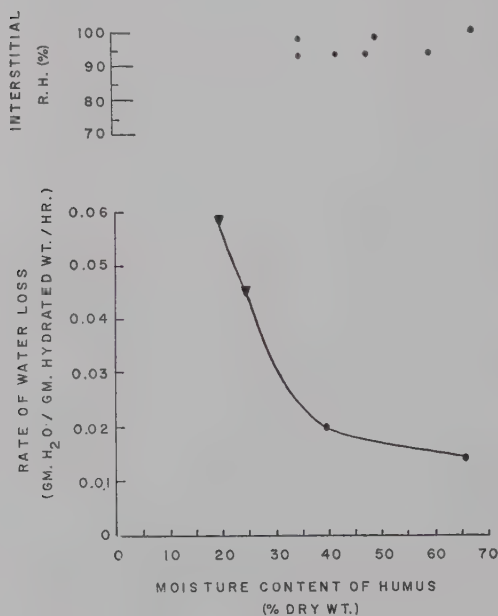


FIG. 3. Relation of rate of water loss by *P. cinereus* to moisture content and interstitial relative humidity of humus. Dots represent salamanders which survived the experiment, triangles those which did not.

The shape of the moisture loss curve is determined by its relationship to moisture tension and interstitial relative humidity. Interstitial relative humidity remained between 90 and 100% in sand in spite of very low moisture content of the substrate. However, theoretical considerations demand that as zero moisture content of the substrate is approached, the interstitial relative humidity must also approach zero. Thamdrup (1939) has in fact presented curves for heath soil and Heatwole (1959) for leaf litter of a beech-maple forest floor in which this is shown to be true. In these studies relative humidity remained high until extremely low values of substrate moisture were reached, at which point humidity decreased sharply. In the present study, conditions of substrate moisture sufficiently low to cause a great decrease in humidity were not encountered in the field.

However, in sand, values as low as 2.8% dry wt were encountered and the sharp decrease in relative humidity must of necessity take place somewhere between this point and zero moisture content. It is precisely in this range that the characteristic curve swings sharply upward indicating that at values below about 3% dry wt, the water is held with a very strong force. At these low values of substrate moisture evaporation into the interstices does not occur and consequently the relative humidity drops causing an accelerated rate of evaporative loss from the bodies of salamanders. This point was earlier defined as the critical level. It has a value of 2.5 atm or a pF of approximately 3.4 for *P. cinereus*. Below this level survival can continue only a few hours.

The high rate of water loss in very dry substrates cannot be attributed to change in rate following death of the salamanders occupying them as the sharp rise in rate of water loss on sand took place before the salamanders died. Also the salamander exhibiting the greatest rate of water loss was still alive at the end of the experiment (Fig. 1).

The water loss curve had the same shape when humus was used as the substrate (Fig. 3). The critical level was between zero and 35% dry wt but as before, data are lacking which would permit expression in tension units for this substrate. The relative humidity of the interstices shows the same relation to the moisture loss curve as occurred with sand. Humidity drops somewhere below a moisture content of 35% dry wt which is the range in which there is an increased rate of water loss from the bodies of the salamanders.

Above the absorption threshold, rates of absorption varied greatly and points on the curves were widely scattered both for humus and sand (Figures 4 and 5) although a correlation between absorption rate and moisture content of the humus appeared to be present. However, in this experiment the salamanders were weighed at the end of the 6-hour absorptive period without taking into account the variable amount of fluid in the bladders of the animals. This was believed to be the source of variation in the apparent absorptive rates of salamanders.

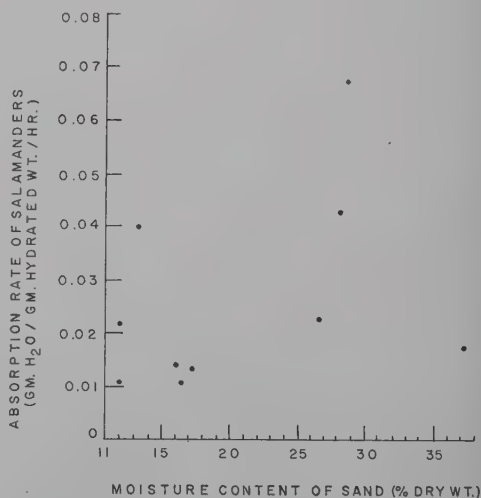


FIG. 4. Relation of rate of water absorption by *P. cinereus* to moisture content of Roselawn Sand.

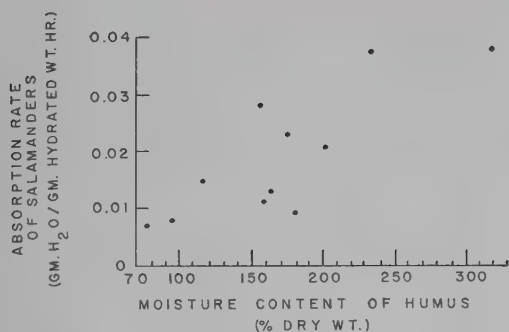


FIG. 5. Relation of rate of water absorption by *P. cinereus* to moisture content of humus.

Salamanders losing water in dry substrates would produce very little urine and hence the curves of moisture loss were not affected by this variable.

EXPERIMENT II

Materials and method

Because of the obvious need of further refinement in experimental technique before a conclusive statement concerning relation of substrate moisture and rate of absorption could be made, the procedure was altered to eliminate the source of error discussed above.

Roselawn Sand was again used but this time the organic substrate was Rifle Peat instead of humus. Two sets of experiments were conducted in constant temperature cabinets, one at 16° C and the other at 23° C. In order to maintain a uniform procedure, the substrates and salamanders were kept for one week prior to their use in the constant temperature cabinet at the temperature to which they would subsequently be subjected in the experiment. During this time the salamanders received no food and were kept on wet paper toweling in order to insure complete hydration. They were then allowed to desiccate until they had lost 15% of their initial body weight and placed in finger bowls filled with substrate. The bowls were stacked on top of each other in such a way that there was no air space between the substrate and the glass bottom of the finger bowl above. During the 6-hour absorptive period, the salamanders were buried in the substrate as previously described. Data from those which were found to have moved to the edges of the container during the experiment so that part of their body was in contact with glass rather than the substrate were discarded. Procedure was further standardized by placing every salamander between 2 paper towels prior to each weighing and pressing lightly on it in the sacral region. This stimulated the animals to void the contents of their bladders.

Separate series of runs were made at 23° C at each of the following levels of substrate moisture: sand at 11.9 and 17.5% dry wt and peat at 137 and 238% dry wt. In addition 2 runs were made with peat at 16° C with moisture values of 206 and 239% dry wt. The number of salamanders in each run ranged from 3 to 11.

Weighing was done in the following manner. Small cylindrical screen cages about 5 cm long and 1 cm in diameter were constructed. Each salamander was placed in a cage and suspended from a hook on the beam of a balance. This method prevented unnecessary handling of the animals and kept them from becoming active

during the weighing process. Animals taken from substrates were quickly brushed clean with a camel-hair brush before placing them in the cages.

Only males were used because preliminary experiments showed a great variability in apparent absorptive rates in females. This was due to the fact that in the early spring when experiment II was carried out, the females were maturing a set of eggs. The consequent increase in body weight was variable depending on the degree of maturity of the eggs and as body weight was used in calculating absorption rates, such a source of variation could only tend to obscure the pattern of water uptake.

Both color types (red and black) were used but no detectable difference in absorptive rate between them was found. Littleford *et al.* (1947) found no difference in the vital limit of moisture loss between the color types of this species. However, on the basis of sampling populations at different seasons, Test (1955) suggests that the 2 types may respond somewhat differently to the increasingly dry conditions of summer.

As the previous experiments had not involved peat, a short experiment was carried out to approximate roughly the absorption threshold on this substrate. Four salamanders were allowed to desiccate and rehydrate as previously described. Samples of peat with moisture contents of 96.5, 204, 312, and 315% dry wt were used. The salamanders on the first sample suffered a loss of moisture whereas those on the latter 3 absorbed water indicating that the absorption threshold for *P. cinereus* is somewhere between 96.5 and 204% dry wt. Reference to the characteristic curve shows that the corresponding tension is between 1 atm and 2.5 or at a pF between 3 and 3.4 (Fig. 2) which agrees with the absorption threshold as determined on sand.

Results

The salamanders on sand with a moisture content of 11.9% dry wt absorbed water at a mean rate of 0.027 g/g/hr, those on sand of 17.5% dry wt at a mean rate of 0.028 g/g/hr. This is reasonable as both values of substrate moisture are relatively close together and lie on the flat part of the characteristic curve. Hence the force with which the soil holds the water and which the salamanders must overcome is approximately the same at both places.

Absorption on peat showed the same pattern. However it occurred at lower rates than on sand with an equivalent moisture tension and at the same temperature. The reason for this is not apparent from the data. At 16° C the average rate of absorption was only slightly higher on peat with a moisture content of 239% dry wt than on that with a moisture content of 206% dry wt (Fig. 6). This is again interpreted as being due to the fact that both values occur on the flat part of the characteristic curve (Fig. 2) and hence the force with which the peat holds water is approximately the same at both levels.

The greater the distance between 2 moisture values on the characteristic curve the greater is the difference in the rate at which salamanders can absorb water. On peat of 238% dry wt salamanders absorbed water twice as fast as they did at the same temperature on peat of 137% dry wt.

There were parallel differences in the proportion of the original loss of water which was recovered. Mean recovery was 87.5% on sand with a moisture content of 11.9% dry wt and 74.0% on that with a moisture content of 17.5% dry wt. On peat at 23° C the mean recovery

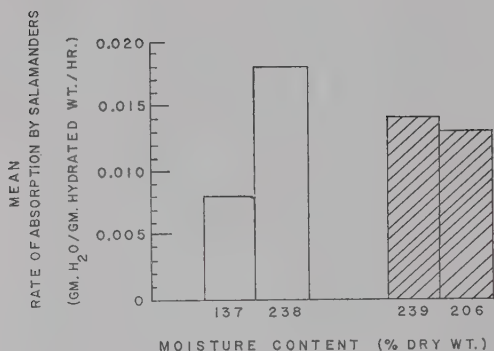


FIG. 6. Mean rate of water absorption of salamanders on peat of various moisture contents. Open bars represent experiments carried out at 23° C, cross-hatched bars represent experiments carried out at 16° C.

was 29.8% when the moisture content was 137% dry wt and more than twice that amount (68.9%) when the substrate moisture was 238% dry wt. At 16° C the average recovery on peat was 36.5% and 48.5% for moisture values of 206% and 239% dry wt respectively.

Temperature influences both percent recovery and rate of absorption as indicated by the higher values obtained on peat at 23° C than on the same substrate with practically an identical moisture content at 16° C (Figure 6).

Small salamanders because of their greater surface area-volume ratio would be expected to have higher absorption rates than larger ones, everything else being equal. However, Cohen (1952) found no correlation between size and rate of absorption in some West Coast salamanders. In the present study the relation of salamander size to absorption rate was not strong and was detectable only when size range was large. The results from each group of salamanders were tested for regression by the method of Kendall Sums (5% rejection level) to see if smaller salamanders absorbed at higher rates than larger ones. The result was negative in all groups except the one on peat with a moisture content of 238% dry wt. This group had a much greater size range (0.09-1.11 g) due to the inclusion of 2 very small salamanders. The size range of the other salamanders used in Experiment II was 0.30-1.12 g. It must be pointed out here, that discarding the data from the 2 small salamanders lowered the mean absorption rate of their group by only 0.001 g/g/hr and neither changes the relationship of that group to others nor alters the conclusions stated above.

DISCUSSION

Plethodon cinereus is a completely terrestrial species restricted to forests where it is found in the soil, in decaying logs and under sticks and stones. It is lungless and therefore highly dependent on the moisture in its environment not only for keeping the body hydrated but also for keeping the skin moist and functional as a respiratory organ. It has no mechanism for preventing evaporation through the skin and its chief adaptation for a terrestrial life other than an egg capable of developing on land is its high vital limit (Littleford *et al.* 1947). Thus, substrate moisture through its effect

on absorption and loss of water is probably the most important factor in the ecology of this species.

At a given location in the forest floor, moisture conditions undergo continual change as influenced by periods of drying interrupted by rains. At one time the substrate occupied by a salamander may have a moisture value above the absorption threshold whereas on other occasions it may be in the limiting range or even below the critical level. When the latter condition prevails survival of the salamander is threatened. However, *P. cinereus* probably stays only a very short time on substrates below the absorption threshold if more favorable substrates are available. Heatwole (1960) found that when this species is subjected to desiccation, the first in a series of behavioral responses is movement to more moist sites. This tends to keep the animals in damp places where water loss from the body is minimal and where absorption can take place.

Temperature is indirectly involved in the water economy of *P. cinereus* as rate of absorption is lower at low temperatures than at high ones. Although not analyzed in the present study, there would undoubtedly also be a lower rate of evaporative loss at reduced temperatures which would tend to compensate for the effect on absorption.

Certain parallels exist between the various levels of substrate moisture discussed here and similar ones used in reference to physiological properties of plants. The absorption threshold is ecologically analogous to the wilting coefficient (substrate moisture at which permanent wilting first occurs in plants) as both express the lower limit of substrate moisture at which particular groups of organisms can maintain an adequate water balance. The wilting coefficient is approximately the same for all soils and has a value of 15 atm (Richards and Weaver 1943) or a pF of 4.2. The absorption threshold for *P. cinereus* lies between pF 3 and pF 3.2 indicating that the absorptive powers of the skin of this species is much less than that of the roots of plants. Even the critical level, which is analogous to the ultimate wilting point of plants, is lower than the wilting coefficient. In addition to this quantitative difference between wilting coefficient and absorption threshold, there is an important qualitative difference as well. The wilting coefficient is not the lower limit of substrate moisture at which plants can absorb water. Absorption may occur at lower values but not at a rate sufficient to replenish the water lost by transpiration (Meyer and Anderson 1952). By contrast, absorption threshold is a very close approximation to the lower limit of substrate moisture at which salamanders can absorb water. This is because evaporative losses of salamanders are very slight within the limiting range and hence the absorption threshold as defined in terms of net gain and net loss is very close to the actual limit at which absorption can take place.

Vascular plants are quite uniform in their ability to absorb water from the soil and hydrophytes, mesophytes, and xerophytes all reduce the water content of a given type of soil to about the same value before permanent wilting occurs (Meyer and Anderson 1952). Whether all species of salamanders show the remarkable uniformity of absorptive power among themselves as do the different species of vascular plants can only be decided by future comparative studies and would provide a fascinating avenue for research.

SUMMARY

Three concepts are introduced and defined. They are (1) absorption threshold, which is the level of substrate

moisture above which there is a net gain in body weight of dehydrated salamanders and below which there is a net loss, (2) critical level, which is the substrate moisture below which water loss from amphibians increases markedly, and (3) limiting range, which includes all substrate moisture values between the above 2 points.

The absorption threshold for *Plethodon cinereus* is between 1 and 1.5 atm moisture tension or a pF of slightly over 3. The critical level for the same species is at approximately 2.5 atm (pF of 3.4) and coincides with the point at which there is a sharp increase in soil moisture tension and decrease in relative humidity of the soil interstices.

Above the absorption threshold rates of water uptake by *P. cinereus* is correlated with soil moisture if comparison is made between soil samples with a sufficiently different moisture content that they do not have similar tensions. Absorption is faster at 23° C than at 16° C. Rate of absorption is weakly correlated with size of animal.

As compared with the roots of vascular plants, salamander skin has weak absorptive powers and both the absorption threshold and critical level for *P. cinereus* are lower than the wilting coefficient for plants. This is compensated for by its behavioral responses to desiccation which tend to keep it in favorably moist situations or to conserve water.

ACKNOWLEDGMENTS

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A STANDARD ENVIRONMENT-CONTROL CHAMBER

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Hendricks and Went (1958) have ably reviewed the wide interest in laboratory facilities for controlled-climate experiments for both plants and animals. In the 1959 report of a special "Biotron" Committee of the Botanical Society of America, in which those authors were included, it was stated with regard to biotron facilities that "... the development of zoological work in this area should begin ... with several local smaller facilities." Some months before these reports appeared, and with no knowledge that such a committee existed, our Zoology staff at the University of Massachusetts had formulated

plans for a standard environment chamber. Rather than "climate control" we are hopeful of obtaining some degree of environment control.

Four of these environment chambers have been in use at the University since April 1960. Since they conform in performance to many of the requirements suggested by the Biotron Committee and should therefore be of interest to many investigators a brief description is presented below.

Each chamber is a self-contained unit with such machinery as refrigeration compressors and steam supply

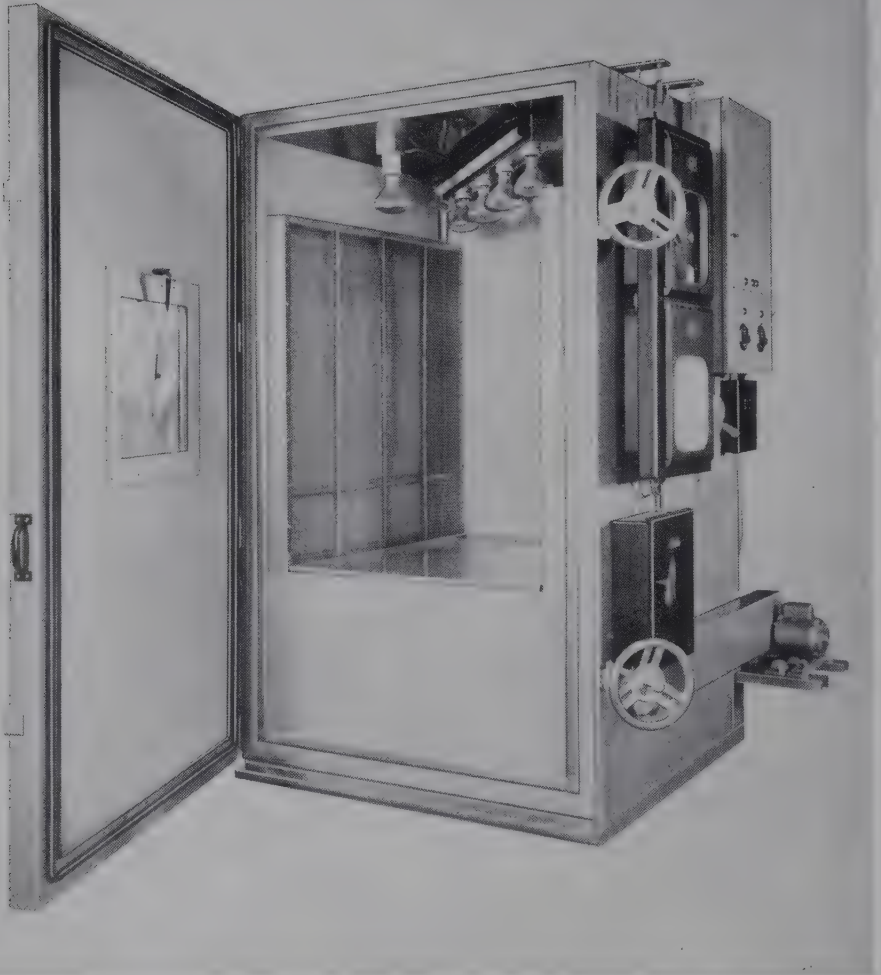


FIG. 1. Environment-Control Chamber. Full front door open to show interior work space. Stainless steel pan forming the floor of the work area may be removed to clean or service heating elements, refrigeration and dew point coils, fan, and steam supply jet. Incandescent and fluorescent lights are arranged in the ceiling to provide uniform distribution of near sunshine intensities and wavelengths of light on the work area.

units mounted on the back and control panels, circuit box, air vent, and access port on the side (Figure 1). Total overall measurements are 68" wide, 78" deep, 96" high.

Refrigeration units for the chambers are water-cooled to avoid raising the temperature of the room in which they are housed. Approximately 13 KW of electrical power per chamber is required for operation at maximum capacity. Compressed air at 20 lbs pressure must be supplied to activate the light control unit.

The free work area is 3' wide $\times$ 4' deep $\times$ 4' high—not including a light bank space of 10". A removable stainless steel pan forms the floor of this space beneath which are housed the refrigeration coils, heating coils,

and dew point coils. Both incandescent (GE Type RS) and 40-watt cool white fluorescent lights are mounted in the ceiling of the work area.

Temperature, humidity, and light are controlled on a 24-hour cycle by easily cut cams. Temperature and humidity are recorded on charts. Light is checked pre- and post experiment by an Eppley pyroheliometer. Test runs of these factors produced the following results:

When all 3 factors are programmed at the same time we have found some difficulty operating at full light intensities with the above tolerances at temperatures below -5°F .

Both aquatic and terrestrial environmental conditions

Factor	Range	Tolerance	Remarks
Light.....	0-140 watts/ft ²	—	Lamps of different wave lengths may be substituted
Temperature.....	-20° F to +200° F	±1.5° F	Slight changes in wiring and gaskets would extend upper limit
Humidity above 34° F.	15%-98% RH	±5% RH	Below 34° F close to ranges listed in Foxboro Dew Point Bulletin (1950)

may be established in the test area. Supports for the clean-out pan are sufficient to hold a 10-15 gallon aquarium. Floor space is adequate to arrange a terrestrial substrate larger than a standard quadrat (2' X 4'). The chambers are relatively sound proof and the observation window can be readily fitted with one-way glass for problems in behavior.

All of the general problems (26 for animals, 31 for plants) listed by the Biotron Committee, and suggested by experts throughout the United States, could con-

ceivably be performed in these environment chambers. Both abrupt and sinusoidal changes in the factors of light, humidity, and temperature may be obtained within ranges which can test most biological functions. The chambers are, furthermore, readily transportable, low in cost (under \$10,000 per unit) and capable of running tests under a wide range of environmental conditions on animals of such diverse size as protozoans and porcupines.

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Special thanks to my colleagues, Dr. L. M. Bartlett, Mr. T. J. Andrews and Dr. D. P. Snyder and also to Dr. S. B. Hendricks, Chief Chemist, U.S.D.A.S., Bethesda, Md., for their pertinent suggestions on the design of the chambers. I am grateful to Mr. Jack Shamroth, American Research Corporation, for his patience and suggested improvements during the construction of the prototype machine.

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ILLUMINATION CONTROL FOR TWILIGHT STUDIES¹

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Levels and changes in light intensity are major environmental factors in the behavior of nocturnal or crepuscular animals. Observational and experimental studies of these animals therefore require light control, on any selected time schedule, of both levels and intensities of light so that night and day lengths and illuminations along with twilight regimes are under control. A number of devices have been developed to effect such light control.

Some light controllers (*e.g.* Bailey and McCabe 1957) have certain built-in limitations, especially in the twilight control, which render them inadequate for our investigations of mosquito behavior. Their stepped brightening and dimming is unsatisfactory because it is so different from nature where it is, of course, continuous. One very effective method of producing a continuously variable illumination is gradually to change the voltage across an electric lamp by means of a variable autotransformer, thereby changing the brilliance of the lamp. If the rotor of this autotransformer is connected to a very low speed drive from a small reversible motor, an automatically simulated sunrise and sunset can be produced. An efficient but somewhat intricate device of this type has been designed (Levin, Kugler and Barnett 1958). We have independently developed an analogous though simpler instrument which is quite adequate for most behavioral studies (Figure 1).

In the apparatus pictured (Figure 2) the autotransformer is chain driven from a 6 RPH reversible motor

with an additional 6 to 1 gear reduction. This reduction (about 1 RPH) creates a sunrise or sunset of 45 minutes duration, which is adequate for our studies. Other gear reductions could be employed to achieve any desired twilight duration.

Fig. 2 illustrates the beginning of sunset. The timer (5) has de-activated the relay (7) thereby closing the

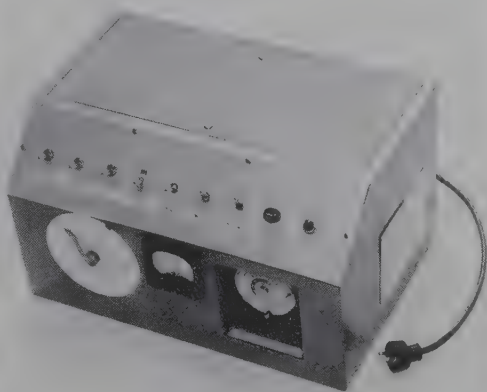


FIG. 1. The light controller for twilight studies.

¹ Contribution No. 110, Entomological Research Center, Florida State Board of Health, aided by grant No. E-1492, National Institutes of Health, U. S. Public Health Service.

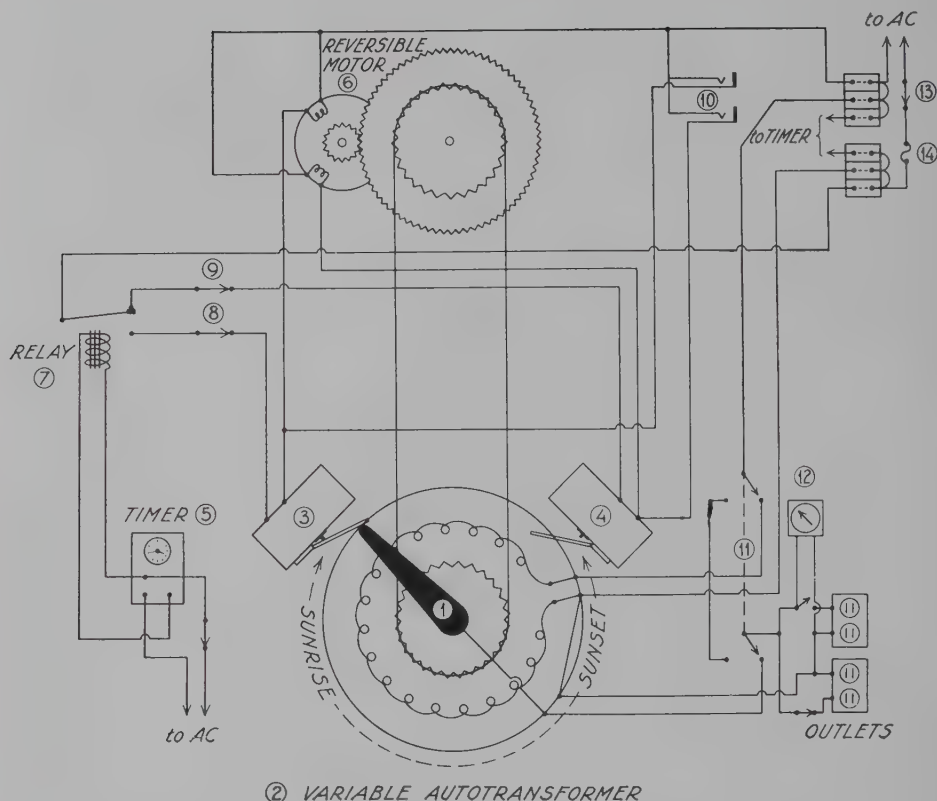


FIG. 2. Circuit diagram for light controller. Positioned at beginning of sunset. See text for description of numbered parts.

circuit through the microswitch (4) which is already closed, thus starting the sunset motor rotation.

The motor (6) turns the rotor of the autotransformer (2) in a counter-clockwise direction, thereby reducing the voltage to the outlets. This action continues until an arm (1) which is attached to the rotor, contacts the microswitch (4). This opens the circuit and stops the motor. The autotransformer maintains this position of minimum voltage until the timer activates the relay and starts the sunrise phase.

At the beginning of the sunset phase when the arm lost contact with the microswitch (3) it closed the sunrise circuit to the relay contacts thereby making this circuit ready for the sunrise phase of the cycle.

The two microswitches set the upper and lower limits of the illumination. They also protect the mechanism by stopping the motor before it attempts to exceed the rotational capacity of the autotransformer. The toggle switches (8 and 9) on either side of the motor circuit make it possible to stop the motor and thus hold the illumination at any light intensity desired during the change. For the reduplication of light intensities with a given set of lamps, the voltmeter (12) is a most useful aid.

The time of the beginning and termination of each light change is recorded on a kymograph. The pens

are fastened to extensions from the movable armatures of two 110 v. AC relays which are plugged into the auxiliary circuits in parallel with each motor winding (10). The purpose of such a record is to know the exact instant of the starting and ending of the sunset and sunrise phases.

Occasionally there is a need for full illumination during periods when the autotransformer is positioned for night or only a partial illumination. To avoid waiting the 45 minutes necessary to complete a sunrise, the double-pole double-throw switch (11) can be used to connect the outlets directly to the 110 v. line. The DPDT switch is essential to prevent a short circuit through a part of the autotransformer winding, and to function as a complete by-pass this switch must be connected as shown.

Four of these instruments have been built in the laboratory. Various departments have used them during the past 2 years with very satisfactory results.

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TOLERANCE OF LOBLOLLY PINE SEEDLINGS TO SOIL MOISTURE STRESS

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Moisture stresses imposed by drought, adverse sites, and competing vegetation largely determine the early performance of outplanted southern pines. The studies reported here indicate that loblolly pine (*Pinus taeda* L.) seedlings can extract moisture from a soil at or below the ultimate wilting point (UWP) of the sunflower. The UWP is considered to be the soil-moisture per cent at which a desiccated plant will not recover after watering. A common grass competitor, little bluestem (*Andropogon scoparius* Michx.), may be even more efficient than the pine in utilizing moisture held at high tensions.

The primary objective of the studies was to determine and compare the UWP of sunflowers, loblolly pine seedlings, and little bluestem grass.

A secondary objective was to estimate how long the pine and grass could survive in a soil reduced to the UWP of the sunflower. Difficulties in visually assessing the death point of the pines led to a study of needle moisture content as an index of mortality, a relationship suggested by Marshall (1931) and Parker (1951).

METHODS

UWP of sunflowers, pine, and grass

A first experiment compared the UWP of sunflowers and loblolly pine seedlings. In January, 1958, one-yr-old nursery seedlings were root-pruned to 4 in. and potted individually in No. 10 food cans, 6 in. in diameter. The cans were filled with 6 in. of screened soil from an eroded phase of Ruston sandy loam—79% sand, 16% silt, and 5% clay. Organic content of less than 2% permitted accurate soil-moisture determinations. The potted seedlings, grown in the greenhouse with ample water, were well rooted by April 30, when sunflower seeds were sown to establish 5 plants in each can.

By June 20, when most of the sunflowers had 6 pairs of leaves, cans with uniform pine and sunflower plants received a final watering and were randomly assigned to the various components of the study. Ten cans were used to determine the UWP of the sunflower, according to the procedure of Furr and Reeve (1945). As the apical leaves wilted, moisture content was determined for each 2 in. soil layer. Twenty-five cans were sealed at the UWP of the sunflower. Of these, 20 were used to determine soil moisture at estimated UWP of the pines. The remaining 5, plus 10 extra unsealed cans, were a check on the reliability of the death-point estimates; the seedlings were watered and observed to detect signs of recovery.

A second experiment compared the UWP of sunflowers, loblolly seedlings, and little bluestem. Single pine seedlings were planted in cans of the same Ruston soil in March, 1958. Clumps of little bluestem were potted separately in May. Sunflower seeds were added to all cans in June. Watering continued through July. Twenty cans with pines were randomly assigned to 3 lots, as were 20 with grass; 5 to determine the UWP of sunflower, 10 to determine soil moisture and root distribution in 3 in. layers when the grass or pines were judged beyond recovery, and 5 to check the reliability of these judgments. As greenhouse temperatures were

high, the cans were placed outdoors after being sealed at the UWP of the sunflower. A black plastic cover shaded the sides of the cans from direct sunlight.

In the root analyses, all roots smaller than one mm in diameter were screened out of the soil, washed, oven-dried, and weighed. It was impossible to separate sunflower roots from those of pine or grass, and the comparisons of root weights assume that the sunflower roots were equally distributed in the 2 lots.

Needle moisture content

Moisture content was determined from 2 composite samples of needles clipped at random from the 20 pines used for UWP determinations in the first experiment. Needles were sampled 2, 13, 19, 27, and 33 days after the average sealing date, and dried at 105°C for 24 hrs. Weighing was to within 0.1 mg; moisture per cents were based on oven-dry weight.

Needles on 2 additional 10 tree lots were sampled during July and August, 1959. The procedure was similar except that the seedlings were potted in a clay loam, the cans were not sealed when the sunflowers wilted, and the needles were dried for 24 hrs at 65°C. The soil consisted of 34% sand, 40% silt, and 26% clay; 15-atm value was 10.70%, as compared to 1.71% for the Ruston soil. The first lot received a thorough last watering on July 17, the second 10 days later. Needles from 3 random seedlings in each lot were sampled at 2- to 4-day intervals until the moisture content dropped to about 180%. After 2 days, and at subsequent 5-day intervals, needle moisture contents were determined for 2 samples from each of 2 randomly selected trees in each lot and the seedlings watered. Twenty watered seedlings served as a control for both lots.

A final test with 10 seedlings growing in a loam soil was made during November and December, 1959.

COMPARATIVE WILTING POINTS

The pine seedlings were able to extract significant amounts of moisture from a soil reduced to the UWP for sunflower (Table I). This agrees with studies of western conifers by Fowells and Kirk (1945) and Stone (1957). Stone reported interspecies differences in ability to withstand moisture stress.

The present comparisons further indicated that little bluestem, a common competitor in abandoned fields over much of the South, may be even more efficient than the pine in utilizing soil moisture held at very high tensions. Whether the difference is due to physiological variations among species of plants (Slatyer 1957), or to the greater ramification of the finer and more numerous grass roots (Aldrich *et al.* 1935, Lane and McComb 1948, and others), is not established. In the pots the grass had a considerable advantage over the pines in absorptive surface, as grass roots were more numerous (Table II). Field excavations of roots indicate a similar situation. Survivals of southern pine seedlings in a heavy bluestem rough are often poor during extended drought, and removal of the rough is often beneficial.

A t-test was made to compare wilting point values (zero to 6 in. depth) for pine in the first and second

TABLE I. Average soil moisture content at ultimate wilting of sunflower, loblolly pine, and little bluestem

Comparison	Cans in Test (no.)	Soil Depth (inches)	Soil Moisture ¹ (pct. by wt.)
<i>First Experiment</i>			
UWP sunflowers vs. UWP loblolly pine ² .	10	0-6	S 1.396
	20	0-6	P .954
Do.....	10	0-2	S 1.206
	20	0-2	P .658
Do.....	10	2-4	S 1.463
	20	2-4	P .948
Do.....	10	4-6	S 1.515
	20	4-6	P 1.257
<i>Second Experiment</i>			
UWP sunflowers vs. UWP loblolly pine ³ .	5	0-6	S 1.378
	10	0-6	P 1.096
UWP sunflowers vs. UWP little bluestem	5	0-6	S 1.464
	10	0-6	G .955
UWP loblolly pine ³ vs. UWP little bluestem	10	0-6	P 1.096
	10	0-6	G .955
Do.....	10	0-3	P .965
	10	0-3	G .841
Do.....	10	3-6	P 1.223
	10	3-6	G 1.067

¹ By t-test for unpaired replicates, all differences except one were significant at the one per cent level of probability. The exception was at the 4-6 in. depth in the first experiment, where the difference was significant at 5 per cent. S=sunflower; P=loblolly pine; G=grass.

² Seedlings grown in south Mississippi nursery from seed collected in central Alabama.

³ Seedlings grown in central Louisiana nursery from seed collected in central Mississippi.

TABLE II. Concentrations of small roots¹

Soil Depth (inches)	OVEN-DRY WEIGHT OF ROOTS	
	Pine (grams)	Little Bluestem (grams)
0-3	1.47 ± .14	1.85 ± .18
3-6	1.27 ± .22	2.27 ± .39
0-6	2.74 ± .28	4.12 ± .48

¹ Average of 10 samples for pine and 10 for grass. Sunflower roots are included.

experiments and for each of the 3 possible sunflower combinations. The values did not differ significantly—an indication that the results from the 2 experiments were consistent.

A soil moisture-tension relationship, developed for the Ruston soil with a pressure membrane, was found to be logarithmic and upon transformation capable of being resolved into an equation of linear coefficients (Fig. 1). The extrapolated curve indicates that the average tension at the UWP of the sunflower is between 21 and 26 atm. This is a considerable departure from the 15 atm value commonly accepted as the lower limit of the availability of soil water to plants. It agrees, however, with the results of Richards and Weaver (1944) who, also using the pressure membrane, found the UWP of the sunflower to be in the range of 20 to 30 atm; and with

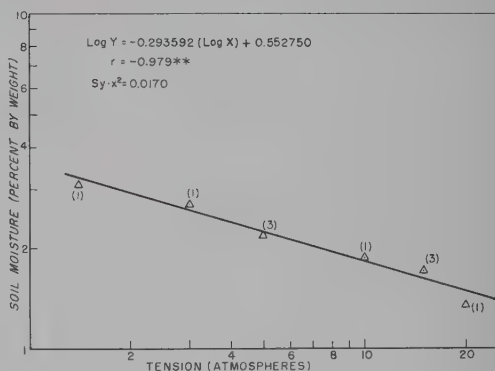


FIG. 1. Soil moisture-tension curve, Ruston sandy loam. Numbers in parentheses indicate pairs of duplicate determinations.

Furr and Reeve (1945), who reported that apical sunflower leaves wilted at an osmotic pressure of 22 atm.

Tensions corresponding to soil moisture at the average UWP of loblolly seedlings and little bluestem range from 50 to 100 atm, if it is assumed that the linear relationship can be safely extrapolated beyond the data.

How long loblolly seedlings survived in a soil reduced to the UWP of the sunflower was not pinpointed, but it was considerably less than the average 9-14 wks reported for 2 western pine species (Stone 1957). Of the 20 pine seedlings used to check reliability of the death-point estimates in the 2 experiments, only 2 recovered—and both received water on the third day after the death of the sunflower. Bluestem check plants were first watered on the eleventh day after the sunflowers had died, and none recovered. However, as indicated below, pine seedlings survived somewhat longer in a heavier-textured soil.

LETHAL NEEDLE MOISTURE CONTENT

The first experiment suggested that 100% moisture (oven-dry basis) approximated the lower limit of tolerance to needle desiccation.

Combined results from the two 10-tree lots of the supplemental studies indicated that seedlings could recover after needle moisture contents were reduced as low as 78%. Needles on 16 of the 20 seedlings that were dried to a range of 211 to 78% regained turgor with subsequent watering and the plants recovered. Seven of these, dried to 104 to 78%, survived for an average of 19 days. The remaining 4 seedlings, with moisture contents reduced below 70% in 18-28 days, did not recover.

The following winter a test with 10 seedlings helped confirm the reliability of needle moisture content as an index of mortality. Seven seedlings reduced to moisture contents of 150 to 95% regained needle turgor and recovered after watering. Three seedlings reduced to a range of 70 to 80% needle moisture content did not. The loam soil in this test (45% sand, 42% silt, 13% clay) had a 15-atm value of 4.09%. Soil moisture at time of needle sampling varied from 1.87-2.73%.

When needle moisture fell to the lethal level the needles not only lost ability to regain turgor but the entire plant died. In not one instance was there recovery by sprouting after subsequent watering. One implication is that the roots may die before the foliage and stem.

Needle moisture per cents derived by drying for 24 hrs at 65°C bear a direct linear relationship to moisture per cent determined by drying at 105°C. Drying at the lower temperature eliminates difficulties caused by plant exudates and permits accurate conversion to moisture per cents based on drying at the higher temperature.

Moisture content of needles from watered plants in all these studies was generally greater than 200%.

SUMMARY

In greenhouse studies, year-old loblolly pine seedlings survived and utilized significant amounts of soil moisture after a sandy loam soil was reduced to the ultimate wilting point of the sunflower.

Little bluestem grass, a common competitor of pine seedlings, further reduced soil moisture by significant amounts.

Ultimate wilting of the sunflower corresponded with soil moisture tensions of 21 to 26 atm. Tensions corresponding to soil moisture at the ultimate wilting of loblolly seedlings and little bluestem may exceed 50 atm.

Loblolly seedlings growing in light- to medium-textured soils did not survive longer than 2-3 wks after moisture within the root zone was reduced to the ultimate wilting point of the sunflower.

Needle moisture content may be a reliable means of identifying the death point of seedlings subjected to high soil-moisture stress. When needle moisture content (obtained as a percentage of dry weight at 65°C) is reduced to about 80%, leaf turgor is not regained and there is no subsequent recovery of the plant with watering.

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MICROFLORA OF DOUGLAS-FIR FOREST SOIL

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AND

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To learn more about microflora in forest soils and its role in formation and decomposition of humus, samples of soil were collected during 1958 from a 25-year-old stand of Douglas-fir near Burnt Woods at summit of the Coast Range, 20 miles west of Corvallis, Oregon. This stand is located on a ridge top at about 800 feet elevation on Astoria silt loam soil.

METHODS AND PROCEDURES

Samples of F and A horizons were composites of three subsamples, each consisting of material from an area one foot square, representatively selected within boundaries enclosing about 20 square feet.

Samples of soil also were obtained from a 20- by 20-foot, level, openly exposed, hard-burned area less than 50 yards from the young-growth stand. Burning had been so intense that dark-brown surface soil was changed to vivid brick-red. Although such burns are typical for western Oregon when logging slash in bulldozed piles is burned, hard burns of this intensity generally constitute

only five per cent, or less, of the burned area, according to Tarrant (1954).

Samples were refrigerated promptly after collection. Analyses were made by standard bacteriological procedures. Dilutions were prepared and determinations of pH were made after moisture was determined. Peptone-glucose agar, acidified to pH 4, was used for fungi; sodium albuminate agar, of pH 7, was used for actinomycetes and bacteria. Quadruplicate plates of appropriate dilutions were prepared for obtaining average counts. Nitrate tests were not made. Collections of soil were started in late January, 1958, and continued at monthly intervals throughout the year.

Data gathered during 1958 were verified by repeating analyses of fresh samples taken at quarterly intervals during 1959.

RESULTS

Microbial Population

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There were extensive fluctuations in numbers of microorganisms from month to month. A definite trend, however, was soon evident, as shown in Figures 1 to 3.

The largest number of molds appeared in soils collected during February for A₁ and A₃ horizons, and in

soils collected during March for A_{00} (L) horizon, as also for burned soil. Litter usually showed the greatest population of molds, except in August, when counts were highest for A_1 and A_3 horizons. Samples taken in October and November also gave low counts, but at these times, differences between horizons were small.

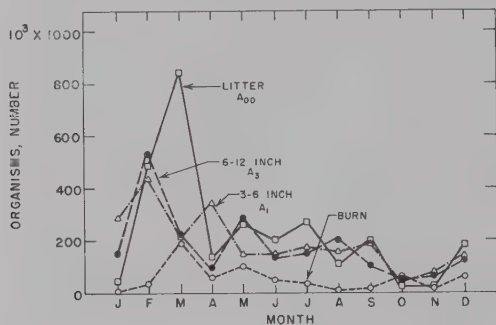


FIG. 1. Seasonal changes in fungi under young-growth Douglas-fir.

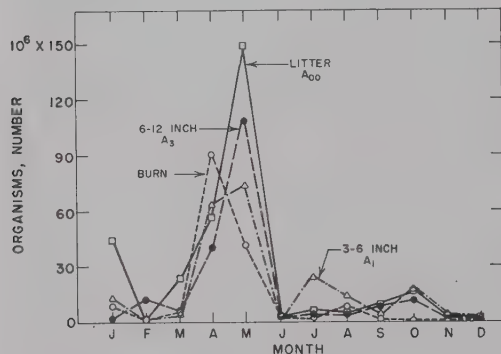


FIG. 2. Seasonal changes in bacteria under young-growth Douglas-fir.

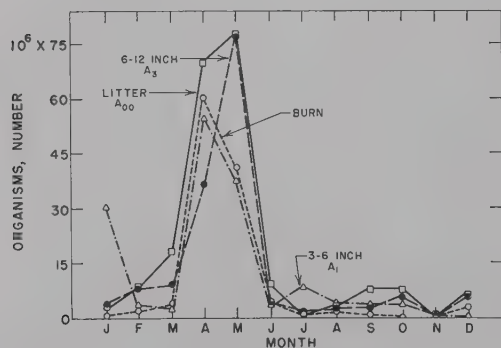


FIG. 3. Seasonal changes in actinomycetes under young-growth Douglas-fir.

In contrast to the population of molds, actinomycetes were most numerous at 3- to 6-inch level (A_1) and in the hard-burned area in April, while samples of litter (A_{00})

and soil at 6- to 12-inch level (A_3) showed highest counts in May. Lowest counts for litter were obtained in July and November. Although specific trends appeared consistent, no simple explanation is apparent for numerical variations of the same group of microorganisms between horizons.

Bacteria were most numerous for all soil samples taken in May, except for hard-burned soil. Count was highest for hard-burned soil in April. Bacteria and actinomycetes also showed increased numbers in October, while counts for molds declined.

Although there were fluctuations in microflora of forest soil from month to month, molds appeared most numerous when counts of actinomycetes and bacteria were low, and conversely. The same relationship was true for hard-burned soil. This result agrees with the findings of Brown and Benton (1930) for soils in Iowa.

Moisture content and acidity of soils are known to exercise considerable influence on microbial population of soil. Relationship of precipitation to soil, moisture, and pH, is shown in Figure 4.

Samples of soil taken quarterly during 1959 showed a quantitative trend similar to that of samples for 1958, rising numerically during the rainy season and falling to a minimum during summer drought. The trend of high and low microbial population for soils under young-growth Douglas-fir likely will continue the same for several years; at least until light and density of stand change with increased age.

Effect of Moisture

During the rainy season, litter had high moisture content, approaching and exceeding 200 per cent, dry basis, for the first third of the year (January through April), even though protected by a dense forest canopy. When precipitation was lowest in July and August, moisture content of litter decreased to less than 25%, which was lower than for the A_1 horizon. Also in July and August, moisture content of the A_1 horizon was somewhat lower than that of the next deeper horizon. During last few months of the year, soil moisture gradually increased as precipitation increased. As might be expected, moisture content of exposed, burned soil fluctuated almost directly with monthly precipitation, but for soil under the dense young-growth canopy, there was some lag, especially in fall months.

The pH of soil showed influence of precipitation, being slightly lower during rainy months than during the dry season. This same trend was apparent for severely burned soil, as well as for soils from stands of young-growth Douglas-fir. These counteracting variations in pH and precipitation further complicate explanation of reasons for differences in microflora from month to month and between horizons.

Effect of Hard Burn

Increase of microbes in hard-burned soil was noticeable in samples taken quarterly during the second year. The comparative trend, however, was similar to that of 1958, except that earliest monthly samples collected in 1958 showed few microorganisms, due to the sterilizing effect of slash burning. Agarics began to appear in the hard-burned soil in December, 1958, about 14 months after burning. This appearance indicated that small, hard-burned, level areas become recolonized rapidly by microorganisms.

Identification of Fungi

Attempts were made to determine monthly variation in species of fungi as they appeared in dilution plates.

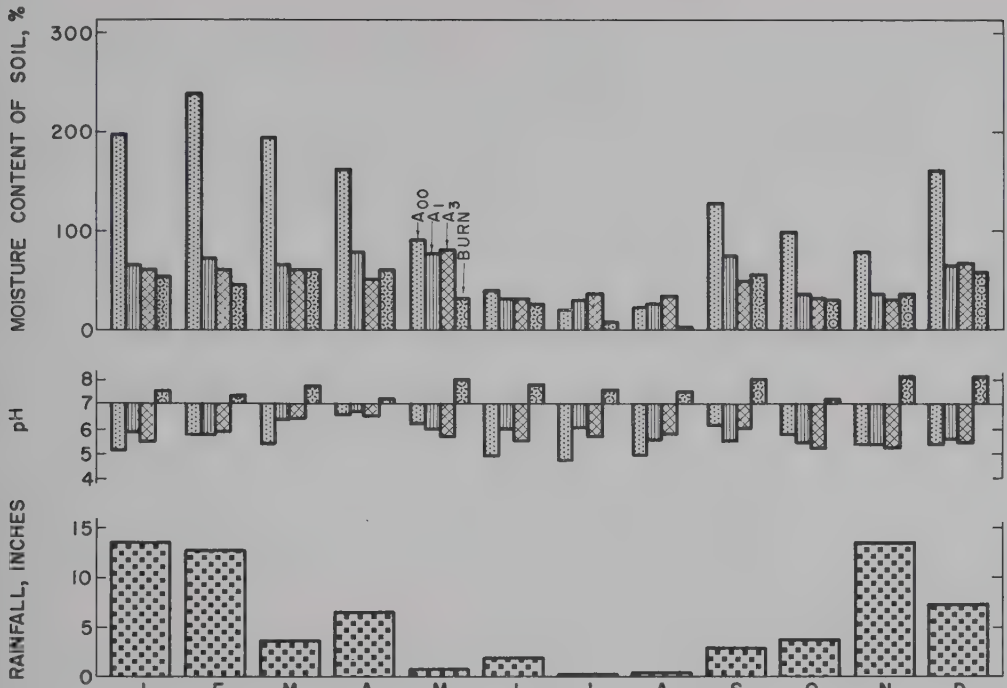


FIG. 4. Seasonal variations in precipitation and in moisture content and pH of soil under young-growth Douglas-fir near Burnt Woods, Oregon, in 1958.

Such procedure soon became too time-consuming in the present study; therefore, only predominant genera and several common species were identified.

Two species of *Penicillium* dominated numerically throughout the series of forest soils, while species of *Mucorales* assumed a secondary role. Percentagewise, *Penicillium* spp. were most numerous in summer and early fall months, while *Phycomycetes* increased during wet months of the year. *Aspergillus* spp. and *Trichoderma* spp. rarely were noted in forest soil.

Litter from Douglas-fir forests regularly contained a black fungus only infrequently observed in the deep horizons. This black fungus has been identified tentatively as *Hormiscium* sp. According to Lagerberg *et al.* (1928) quoting Lindau, *Hormiscium* species are only specific mycelial stages of *Ascomycetes*. However, the same author stated that Negar found that *Dematiu pullulans* mycelium could not be distinguished from that of *Hormiscium* sp. Lagerberg *et al.* (1928) place *Hormiscium* sp. in *Hormonema*. This example indicates the difficulties encountered in naming correctly different species of fungi encountered in studies of dilution plates. *Hormodendrum* sp., a similar-appearing fungus, also was common in dilutions of litter from Douglas-fir.

Most characteristic fungus, especially at the 3- to 6-inch level (A_1 horizon), was identified tentatively as *Phytophthora* sp. It also was found to lesser extent in the A_3 horizon. In peptone-glucose agar, this *Phytophthora* developed a radiating, or spoke-like, characteristic and was pure white in color. Its growth was somewhat appressed (Fig. 5). Spherical, sporangia-like growths developed in cultures a month or more old.

Identity of this fungus as a *Phytophthora* sp. is still



FIG. 5. A fungus like *Phytophthora* that showed radiating growth in dilution plates of forest soil from a stand of young-growth Douglas-fir. Note antagonistic reaction of a *Streptomyces* on upper part of plate.

questionable, even after observing its growth habits on several other media.

A *Phythium* sp. was common in all horizons of forest

soil, especially in late spring, while *Fusarium* spp. were most common in collections made during summer and fall.

The most common *Mucor* sp. observed in both burned and unburned forest soil was identified as *M. ramannianus* A. Moeller, although according to Gilman (1957), this mold has not been reported in soils in the western United States. *Rhizopus nigricans* Ehrenberg occurred occasionally.

Two principal species of *Penicillium* most frequently observed were identified as *P. expansum* (Link) Thom, and *P. cyclopium* Westling. *Penicillium* spp. predominated, especially in collections of soil made during summer months.

In general, fungal flora of soil under young-growth Douglas-fir was fairly constant qualitatively, and contained few dominant genera as compared to hard-burned soil.

In addition to presence of species of *Penicillium* in burned soil, there also were present *Gliocladium*, *Cephalosporium*, *Acrostalagmus*, *Aspergillus*, *Spicaria*, *Trichoderma*, *Stemphyllium*, and several unidentified phycomycetes, besides *Mucor ramannianus*. This circumstance might be expected for soil that is being recolonized after near-sterilization from heat. The tentatively identified *Phytophthora* sp., however, was not found in burned soil. Usually in most dilution plates there were several colonies of nonsporulating fungi that defied identification, except as *Mycelia sterilia*.

An occasional colony of what appeared to be an atypical form of *Rhizoctonia* also was observed, as well as a white fuzzy fungus forming white sclerotia. Identification and abundance of fungus species in these soils requires more study before definite trends of seasonal species can be established.

No attempt has been made here to classify bacteria isolated on dilution plates. All actinomycetes encountered appeared to be Streptomycetes, which ranged in color from white to pink, yellow, brown, and red, with an occasional purple or black colony showing. Probably some *Nocardia* and *Micromonospora* were present. This group of higher bacteria, characterized by ability to attack lignins and other forms of resistant organic matter, requires additional study for thorough understanding of their distribution and ecological significance in forest soils.

Detailed study of bacteria and actinomycetes of forest soils of the Pacific northwest is needed. Their identity may be less important than their interaction with other microorganisms, as indicated in Figure 5.

SUMMARY

On a seasonal basis, the greatest number of microorganisms found in soil from a young-growth Douglas-fir stand occurred from February to April. Generally, the highest percentage of molds occurred when bacteria and actinomycetes were low, and conversely. Soil from an adjacent burned area showed the same trend in micropopulation; however, it was much reduced immediately after burning and did not begin to approach normality until 14 months later.

Fusarium spp. appeared numerous in late spring, and *Phythium* spp. were most common in summer and fall. Additional observation of many molds, especially *Phytophthora* spp. still are required.

Hard-burned soil acquired complex microflora about a year after being burned and in the second year began to exhibit a population characteristic of unburned soil.

The microflora of forest soils greatly increased in numbers during rainy periods and decreased during times of drought. This variation emphasizes the importance of standardizing microbial studies with season of year, type of soil, and method of sampling.

The pH of soil appeared to vary inversely with rainfall; it was slightly lower during summer months, when precipitation is lowest, than during winter, when soils are wettest. This trend was exhibited by both burned and unburned soils.

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SOME ASPECTS OF THE REGENERATION HABITS OF THE AMERICAN BEECH¹

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INTRODUCTION

The American beech (*Fagus grandifolia* Ehrh.), like several other tree species, reproduces both from seed

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and by the production of sprouts from roots. The conditions which favor or adversely affect each type of reproduction are incompletely known. The present investigation, carried out during the summers of 1958 and 1959, had as its purpose the further understanding of regeneration tendencies in beech, and the general conditions associated with observed variations. The emphasis was put on beech in Wisconsin, because many

TABLE I. Summary of Beech Reproduction in Primary Study Areas

Stands	Dominant trees	SEEDLING		SPROUT		Seedling/ sprout	SAPLING	
		Density	Frequency	Density	Frequency		Density	Frequency
N. E. Wisconsin ¹ ... (5 stands)	Beech, S. Maple	0.1-2.4	10-85%	0.05-0.4	5-25%	87/13	0.25-1.35	12.5-75%
East Central Wisc. (7 stands)	S. Maple, Beech	0.02-0.5	2.5-27.5%	0-0.15	0-5%	57/43	0-0.55	0-45%
S. E. Wisconsin... (7 stands)	Beech, S. Maple	0-0.1	0-5%	0-0.3	0-20%	2/98	0-0.5	0-35%
Warren's Woods... (S. W. Mich.)	Beech, S. Maple	0.62	32.5%	none in quadrats		—	0.3	25%
A. B. Williams... (N. Ohio)	Beech, S. Maple	3.2	67.5%	0.2	7.5%	94/6	0.18	12.5%
Tionesta... (N. W. Penn.)	Beech, Hemlock	13.5	87.5%	0.6	37.5%	96/4	0.6	25%
Percy Warner... (W. Tenn.)	S. Maple, Beech	0.15	10%	none		100/0	none in quadrats	
Turkey Run... (W. Cent. Ind.)	Beech, S. Maple	0.10	10%	none		100/0	no data	

¹All values for density and frequency in Wisconsin are minimum-maximum ranges.

stand locations and the phytosociology were well known to the author, and also because it was known that a considerable variation in numbers of seedlings and sprouts could be found.

METHODS

In Wisconsin most of the stands had been studied previously (Ward, 1956, 1958), thus considerable information on trees (4" dbh or greater), saplings (1"-4" dbh), and seedlings (less than 1" diameter) was available. The random pairs method (Cottam and Curtis 1948) had been used for trees, providing reliable information on the most important trees in a stand. Thus no further analysis of the tree stratum was made. For new stands, in Wisconsin and out of the state, the quarter method (Cottam and Curtis 1956) was employed, omitting distance measures and tree diameters. Experience showed that tree size and spacing did not vary greatly in the woods chosen for the study. From 40 points (160 trees), relative density and relative frequency were computed.

For saplings it was decided to obtain additional data, using a series of 20 plots each 16 m x 1 m. These were sampled by holding a meter stick directly across the front of the body and pacing the 16 m distance, sighting on a distant tree to approximate a straight line. Although not so precise as measured and staked plots it seldom happened that there was a question as to whether a sapling was in or out of the quadrat area.

Since in my previous analyses of seedling-sized individuals no differentiation had been made between true seedlings and root sprouts, the tree reproduction of less than one inch diameter was sampled by one meter square quadrats. In most instances 40 such quadrats were taken. In several stands the occurrence of reproductive units in the quadrats was so low that more information on the relative importance of true seedlings and root sprouts was desirable. For this a tally was made of the two types encountered while walking at random through the woods, and the total count (usually 100) was put on a relative basis.

The distinction between true seedlings and root sprouts could frequently be made visually, based upon cotyledons or cotyledon scars, or the superficial position of a root-sprout junction. For many other individuals the de-

cision as to sprout or seedling was made by searching with the fingers down along the stem below the ground level for such a junction.

Complete maps were made of the sprouts arising from certain individual trees isolated from other beech. Direction and distance from the parent, and stem diameter were recorded. Where browsing or other causes had resulted in many small shoots coming from essentially one origin the group was treated as a unit. Usually the age of the parent tree was found by making a core ring count. To compare early growth rates some seedlings were removed, and a few sprouts were cut.

General observations on the environment were supplemented with data on soil nutrient content, weight/volume ratios, and water retaining capacity of the A₁ horizon. The nutrient analyses were made by the University of Wisconsin Soils Laboratory, employing colorimetric techniques. Pulverized soil samples were used to determine weight/volume ratios, and the same materials were used in Hilgard cups for determination of water retaining capacities.

Light readings in foot candles were obtained by use of a Weston Photometer and a Brockway light meter. Readings were taken as close to mid-day as possible, and when the sun was fully exposed.

RESULTS

Wisconsin Studies

A total of 19 stands was studied in Wisconsin, slightly more than half of which had northern hardwood-conifer elements (Fig. 1). The pattern of seedling abundance showed a definite increase in a general direction of south to north (Table I); no true seedlings were found in three of the southern stands. This may be compared to an average of 2.4 seedlings per one meter square quadrat in one of the northern stands. Based primarily upon the general abundance of seedlings, the Wisconsin stands were assigned to three groups. This allowed a summary analysis of geographic patterns in reproductive habits (Fig. 1). In the southern group true seedlings exhibited an average frequency of 1.4 per cent, with an average count of only two out of 100. In the central stands the frequency was 9.4 and counts averaged 57 out of 100; while in the northern stands the

dbh (age range, 59-104 yrs) the average annual diameter increment was about 2.7 mm.

Studies Outside of Wisconsin

The studies outside of Wisconsin also revealed considerable variation in the reproductive habits of beech (Table I). At Tionesta, an extensive virgin hardwood-conifer forest in north-central Pennsylvania, an unusually dense population of beech seedlings was observed. With an average of 13.5 beech seedlings per quadrat, the density greatly exceeded that recorded at any other stand visited in the study. The great majority of the seedlings had germinated the previous spring, and only one out of the 541 counted in the quadrats was more than one foot high. The mor-type humus layer was overlain with heavy litter and underlain with a silty-loam soil. Germination usually occurred in the lower portion of the litter.

The density of beech seedlings in stands of western and southern Indiana, western Kentucky and western Tennessee was in sharp contrast to that at Tionesta. Typical were the data obtained in a stand dominated by large beech in Turkey Run State Park, Indiana. In 40 m-sq quadrats only 4 seedlings were recorded; this may be compared to 156 seedlings of sugar maple. The soil in all of the stands of this general area had a definite mull humus, with a minimum of duff and litter in early summer.

A further variation in the pattern of seedling production was seen in the beech "gaps" along the ridges in the Great Smokies. Here no beech seedlings of any size were found.

The observed variation in numbers of root sprouts was equally as great as for seedlings. At one extreme was the dense cluster of root sprouts of about one inch diameter and 5 feet high that develops in portions of the beech "gaps." A sizeable proportion of the sprouts, though standing erect, are dead.

Contrarily, root sprouts were not found in any of the stands near the western border of beech. Superficial lateral roots of beech were abundant in these stands, and many instances of surface abrasion were noted, which in other areas very likely would have produced some amount of sprouting. Ware (personal communication) has reported the absence of root sprouts in stands of northwestern Louisiana.

Numbers of seedlings and saplings somewhat intermediate to the extremes mentioned above were observed in several stands, including Warren's Woods in southwestern Michigan, William's Woods in northern Ohio, and stands in northern West Virginia and in the vicinity of Washington, D. C. In each of these both seedlings and saplings were located without difficulty.

DISCUSSION AND CONCLUSIONS

Any consideration of seedling numbers must take into account the tendency on the part of many tree species to have intermittent years of heavy seed production. Beech seems to have such a pattern, at least in some of the areas. The observations at Tionesta, where first year seedlings were very abundant, indicated the occurrence of a heavy mast crop the previous season. The possibility exists, therefore, that in the three Wisconsin stands in which beech seedlings were not found that an intensive search in other years might locate a few or even several seedlings. The fact that no individuals of beech below one inch diameter of seed origin were found in these stands, however, indicates that seedlings probably have not been produced in any abundance for

some time. If the numbers produced are sizeable in some years, which seems unlikely, there is still an important survival difference between these and more northern woods of the state.

Certain factors seem to correlate with the greater production of beech seedlings in northeastern Wisconsin as compared to more southern stands in the state. The climate, though not greatly different, is on the average somewhat cooler and probably more moist to the north, resulting in a slightly more favorable P/E ratio (Ward 1956). Outside Wisconsin the general sparsity of seedlings in stands near the west-central edge of the range, where moisture conditions are least favorable, makes this factor seem worthy of further investigation. Ware (personal communication) reported seedlings abundant in a beech stand in northwestern Louisiana, an area near the western border of beech but without similar moisture stress.

Evidence from the Wisconsin stands suggested the possibility that germination and early growth of beech might be favored by the somewhat more moist and less compacted conditions usually found in humus tending toward a mor rather than to a mull type. The great number of seedlings associated with the mor humus at Tionesta is perhaps indicative of such a relationship, although the scarcity of older seedlings leads to doubt as to any particular benefit much beyond germination. It is a fact that most of the stands with a mull humus had only small numbers of seedlings; Warren's Woods in southwestern Michigan was one exception.

A factor of obvious importance to the number of seedlings in a stand is the production of viable seed. Although this study was not made at a time when mast counts would be very informative, it has been the author's experience through the several years of visiting the Wisconsin stands that beech woods in the southern part of the state had a great majority of empty seeds, and although the number of full seeds in the more northern stands was not large, the difference was noticeable. The problem of differing seedling numbers is then shifted from survival to the causation of differences in viable mast production.

The fate of full seeds may in some instances be a matter of considerable importance. Since beech mast is a choice food for several animals, especially birds and rodents, a sizeable seed crop is surely required to more than balance the biotic destruction. At Tionesta, where the seedlings were very abundant, there was some evidence of caching on the part of animals. Although such burial may benefit germination and initial growth, the tightness of many of the groups would seem to preclude extended survival for most individuals.

Even advancing to the small seedling stage the chances of being eaten are perhaps almost as great as for the seeds. Browsing animals likely find the soft tissues of young seedling growth as palatable as the tips of stems on older plants; recovery by small beech seedlings is probably the exception. In contrast much evidence was found that sprouts can withstand repeated browsing, with perhaps even some kind of stimulation for additional production of sprouts. The animal factor is potentially a very important one, but whether it has a strongly differentiating effect on numbers of seedlings vs. sprouts is not known.

In the stands studied in Wisconsin and other Lake States, root sprouts with minor exception arose from lateral roots which were near or at the surface. The fact that mechanical abrasion seems to stimulate root sprouting was evidenced by rather consistent observations

of sprouts coming from lateral beech roots crossing paths. That such stimulation is not always necessary, however, was indicated by the finding of young sprouts arising from deeply buried roots in mid-elevation stands in the Great Smokies.

SUMMARY

The production of reproductive units by the American beech was studied in 19 stands in Wisconsin and in several stands in other states. Seedlings were rare in beech stands of southeastern Wisconsin, but were progressively more abundant in stands to the northeastern part of the state. Root sprouts were numerous in the southeastern stands and slightly more abundant in stands to the northeast.

Outside of Wisconsin seedlings were abundant in stands in the Lower Great Lakes area, but were scarce in stands near the west-central border of beech. Root sprouts were absent from all stands visited in the latter area, but were the only type of reproduction observed in the beech "gaps" of the Great Smokies.

The data on the water retaining capacity of the A_1 horizon in the Wisconsin stands suggested a positive correlation with increasing numbers of seedlings, although there were notable exceptions. Soil chemical analyses (Ca, Mg, K, P) of Wisconsin soils showed no correlation with seedling numbers. Weight/volume ratios of the A_1 horizon, indicative of bulk density, were noticeably lower in stands having greater seedling numbers. In stands where the humus was an intermediate

mor-mull type seedlings were often abundant, but in most stands with a mull type of humus seedlings were scarce.

Usually only a relatively few trees in a stand produce sprouts, with the number of sprouts consistent with the size of the parent. Eighty-one sprouts of one inch diameter or less were mapped around a parent tree of 18" dbh and 90 years of age; all were within a radius of 24 ft from the parent. The production of sprouts appeared to be favored by a shallow accumulation of litter and duff, although young sprouts were found coming off from rather deeply buried lateral roots. Early growth rates suggest that sprouts may have some advantage over seedlings in this regard, and the ability to withstand browsing may provide an additional advantage of importance.

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A PEAT SAMPLER FOR COMPACT DEPOSITS

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The deposits lying below salt marshes often have properties which render inadequate the conventional peat samplers with spring type locks. These deposits may be thick and highly compressed at the lower levels, but even at the upper levels shell beds, thick clay and sand layers may offer great resistance to the sampling device. Under such conditions, the spring of the Davis type peat sampler breaks or bends when the tool is subjected to strong pressure while locked in the open position. In addition, highly compressed deposits often prevent the spring from engaging in the manner necessary to lock the sampler in the open position.

During the summer of 1959, I sampled a salt marsh deposit using a Davis type sampler. I soon had to discontinue sampling until a device was constructed that would function in the deposits encountered. Figure 1 shows the basic features of this device.

Its primary purpose is to obtain samples where the deposits are hard, compressed, and thick. Its design emphasizes durability and eliminates the weakness of the spring of the Davis type sampler so that it can be subjected to great force during all phases of the sampling process. It can be quickly and economically built, replaced, and repaired and its durable construction permits the obtaining of a rather large sample. The sampler I used obtained a core having a diameter slightly in excess of 1 in.

Figure 1 shows the sampler, which consists of a barrel (1) of relatively thin steel tubing sharpened at one end, a steel bushing (2) welded inside the upper barrel (1), a key-way (3) cut through the bushing (2), a driving coupling (4), a shaft (5) screwed and pinned into the driving coupling (4), a key (6) welded and pinned to the shaft (5), and a driving point (7) screwed and pinned onto the shaft (5). The driving rod (8), not actually a part of the sampler, is best made of segments of steel rods of convenient lengths having a tapered or otherwise specialized thread.

For best results the parts should be made of tough steel, preferably stainless, in sizes approximately proportional to those shown in the diagrams. However, I had good results with a driving rod (8) of $\frac{3}{8}$ in. pipe, a driving coupling (4) from a $\frac{3}{8}$ in. to $\frac{1}{2}$ in. reducer coupling, a shaft (5) of $\frac{1}{2}$ in. pipe, and a driving point (7) of scrap metal turned down on a lathe. A bushing (2) with a key-way (3) was cut from steel pipe and placed in the upper part of the barrel so that it protruded slightly. A weld was then placed around the lateral protruding walls of the bushing (2), thereby fixing it to the barrel (1). This weld was supplemented by drilling a few holes through the barrel (1) and partly into the bushing (2), and then filling these with a weld.

The device is driven to the sampling depth in the closed position (Fig. 1-A). At this depth, the operator pulls up on the drive rod (8) until the driving point (7) contacts the bushing (2). At this point, the key (6) has cleared the key-way (3), and by turning the drive rod (8) one half turn, the key (6) is positioned 180° from the key-way (3). Downward pressure on the drive rod (8) causes the key (6) to contact the upper surface of the bushing (2) and pushes the barrel (1) into the deposit, thereby cutting out a sample.

The key (6) replaces the spring of the Davis sampler

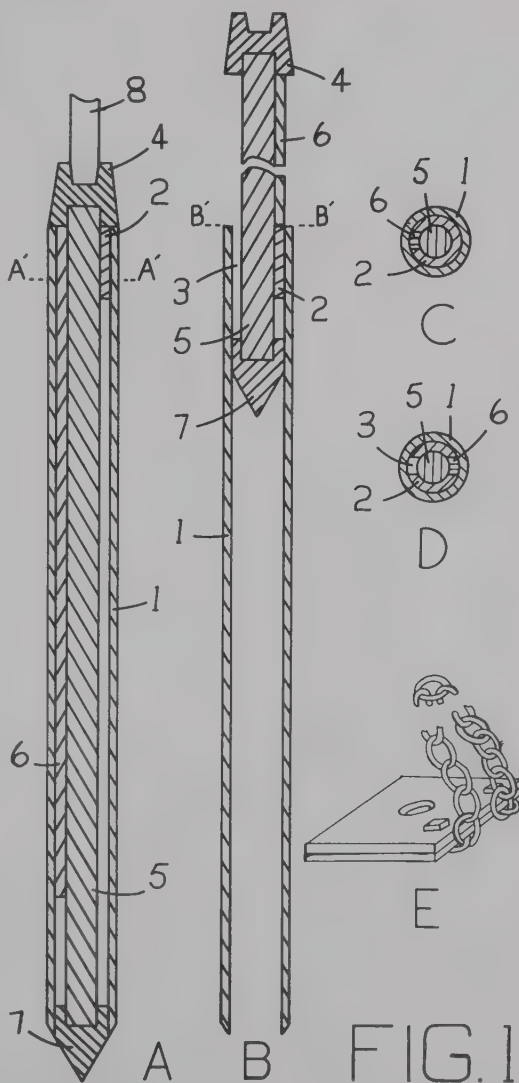


FIG. 1. A. Longitudinal sectional view of sampler illustrating position of parts when sampler is being driven into deposits. B. Position of parts after sampler has been opened and locked in preparation for cutting a sample. C. Cross section of sampler on plane indicated by A'-A' indicating position of parts when sampler is being driven into deposits. D. Cross section of sampler on plane indicated by B'-B' illustrating position of parts when sampler has been opened and locked in preparation for cutting a sample. E. Device for gripping the drive rod.

and can withstand much more physical abuse than the latter. A slight burring of the key (6), where it

contacts the bushing (2), can usually be remedied by filing.

When the sampler is pulled up, the driving point (7) contacts the bushing (2). Because these two parts are well secured, the sampler may be retrieved under great force.

A sledge hammer or steel post driver may be used to drive the sampler down providing that the top of the drive rod is capped. Retrieving the sampler is accomplished by lever, fulcrum and a device for gripping the drive rod. This gripping device (Fig. 1-E) permits the operator to maintain his position at the end of the lever and bring up each length of rod by a pumping action. The gripping device consists of two square $\frac{1}{4}$ in. thick steel plates bolted together. A chain is attached

by these bolts, and the chain attaching point must face downward. The drive rod passes through the center holes in the plates. When the operator raises his end of the lever, the plates balance and slide down the rod, but when he forces down on the lever, the plates bind and grip the rod. The device functioned well on the $\frac{3}{8}$ in. pipe but has not been tested on very hard steel rod.

All driving rods must be screwed together tightly, so they will not interfere with the positioning of the key. Tapered or other types of specialized threads are best for this. An assortment of rod lengths should be used. By using the longer rods whenever possible the number of couplings is reduced.

WINDFALL IN FOREST ECOLOGY

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Often in the history of science observation of a "new" phenomenon or development of a new theory results in the subsequent recognition of prior statements which have substantially the same import but which failed to gain attention in their time. In many instances the earlier commentators did not fully appreciate the importance of their observations or ideas and there is danger of reading modern views which they did not actually appreciate into their statements. In other cases their observations are prescient statements of modern views which were, however, not made in a cultural or scientific context in which they were timely (Taton 1958).

Recently the importance of windfall or the uprooting of forest trees has been emphasized by ecologists and soils scientists. Stephens (1956) notes, "For many years the uprooting of trees has been recognized as a natural phenomenon. As such, it has usually been regarded as one of freakish occurrence noted for its direct and catastrophic effect upon the trees immediately affected. Uprooting it seems has seldom been considered with enough perspective to reveal its basic relationship to the forest." Later he comments on uprooting in the light of recent work, including his own excellent study: "its role becomes that of a natural forest process rather than a single event in the life history of a forest stand." Stephens cites as causes, root systems weakened by specific root pathogens, fire, water erosion plus seasonal winds or combinations of these.

In the writings of the Swedish naturalist Peter Kalm (Benson 1937) based on his "Travels in North America" in the mid-eighteenth century, Kalm commented as follows:

Windfalls. On travelling through these woods, I purposely tried to find out, by the position of the trees which had fallen down, which winds are the strongest hereabouts. But I could not conclude any-

thing with certainty, for the trees fell on all sides and lay towards all the points of the compass. I therefore judged, that any wind which blows from that side where the roots of the tree are weakest and shortest, and where it can make the least resistance, must root it up and hurl it down. In this manner the old trees died continually, and are succeeded by a younger generation. Those which are thrown down lie on the ground and putrify, sooner or later, and by that means increase the black soil (humus), into which the leaves are likewise finally changed. The leaves drop abundantly in autumn, are blown about by the winds for some time, but are finally heaped up and lie on both sides of the trees, which have fallen down. It requires several years until a tree is reduced to dust. When the winds tear up a tree by the roots, a quantity of loose soil commonly comes up with and sticks to them for a time, but at last it drops off and forms a little hillock, which is afterwards augmented by the leaves. In this way many holes and mounds are formed.

Kalm's recognition in the mid-eighteenth century of the continuous nature of windfall and the successional effect on the forest, as well as the effect of the tipped up roots on the soil with the formation of mound and pit, pinpoints the essentials of windthrow as recognized in modern forest ecology.

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MORTALITY OF FINGERLING SHINERS RESULTING
FROM BECOMING ENTANGLED IN THE ALGA *HYDRODICTYON*

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Water net (*Hydrodictyon reticulatum*) is a colonial, green alga with an unusual growth form. The individual cells in the adult plant become 4-5 mm long and form a network (Fig. 1) with a mesh size of 6-8 mm in older plants. The colony forms a sac measuring up to 50 mm in diameter and 200 mm in length. The number of cells in a young colony is the same as in the adult colony but those of the young one are much smaller and consequently the mesh size is smaller.



FIG. 1. A 35 mm golden shiner caught in the network of *Hydrodictyon reticulatum*. (Photograph by Harry Sharpe)

Water net is characteristic of hard waters. Some of the masses on which this report is based extended upward from the bottom to a height of one to two feet.

In this study I observed that the network of the older colonies functions as a gill net in which large numbers of small fishes became entangled. I also noted that the young, sac-like colonies have a gas bubble in their closed end and this floats the young colony upward and supports it during early development.

For aid in making the various observations reported here the author is indebted to his wife Sue D. Lewis.

Field observations indicate the efficiency of the alga in entangling fish. During the first week of August (1960) 2,000 adult golden shiners (*Notemigonus crysoleucas*) were stocked in a $\frac{1}{2}$ acre hatchery pond. Ninety per cent of this pond was 2½ ft deep and the remaining 10% was 3½ ft deep. The pond was supplied through most of the summer with 10 gal/min of hard water (methyl orange alkalinity of 237 ppm.) During my observations the water remained clear and I could observe the distribution of the young fish and their immobilization in the algal net.

Shortly after stocking, the shiners produced a good spawn estimated at 100,000 fingerlings. These were evenly dispersed around the periphery of the pond, which is a normal behavior for these young fish. The fish were fed daily and by Sept. 2, were responding normally

to feeding, i.e., collecting at the feeding site. By the second week of Sept. they ceased to move to the feeding site and accumulated along the south side of the pond even though feeding was continued on the north side. During the last week of Sept. there were numerous dead fingerlings in algal masses. By Nov. 5, there was a pronounced accumulation of fish in the southeast corner and an increased number of dead fish in the algal masses there. Detailed examination of the cause of death was undertaken.

Except in the deep water at the west end and in the southeast corner, the pond supported a heavy growth of water net. In the clear area in the southeast end the young fish were concentrated. No fish were ever observed in the areas of heavy growth of the water net.

In the area where the young fish were concentrated there were isolated masses of water net. In these masses and in the water net around the periphery of the area of fish concentration, numerous shiners 30-40 mm long were caught in the algal mesh. Some of these fish had been dead for a long time. The fish became entangled in the algal mesh in the manner in which they would be caught in a gill net. They started through the mesh, but sometimes the mesh size was large enough for the fish's head but not its body (Fig. 1). The fish was trapped in the water net and in many cases was unable to withdraw. Disturbances in the region of concentration frightened the fingerlings; they swam about in the clear area but would not swim into the area of dense growth even though there was open water above most of it. When the fish were disturbed they swam past the isolated masses in the clear area and past the growth on the periphery of this area, and a number of them were caught.

A mass of the water net was placed in a concrete tank 7.3 m long and 0.9 m wide, containing 20 cm of water. In the tank were shiners from 50-250 mm long and a number of mosquito fish (*Gambusia affinis*). When the fishes were frightened into the algal mass, even the movement of the larger fish was greatly impeded by the netting. A number of the smaller shiners and adult mosquito fish were entangled and were unable to extricate themselves. The fish were undisturbed for 3 hrs, after which time additional mosquito fish had been held.

Hydrodictyon may derive nutrients at least indirectly from the fishes that are trapped and eventually die and decay. Algae in general show rapid response to fertilizers.

Hydrodictyon may have a significant effect on populations of small fishes. In this minnow pond the alga appeared to reduce the population of fingerling shiners and greatly affect their distribution within the pond. In deeper lakes water net might occupy the shallow water areas utilized by young fish of most species. Under such conditions young fish might suffer pronounced mortality.

SUMMARY

Water net (*Hydrodictyon reticulatum*) was observed to effectively entangle fingerlings of the golden shiner

(*Notemigonus crysoleucas*). Some shiners were unable to extricate themselves and died. The shiners exhibited a marked avoidance reaction to the alga. The algal

colonies grow in a sac-like form. The young colonies have gas bubbles in the closed end of the sac and float at the water surface during their early growth.

BENEFITS TO UNDERSTORY FROM CANOPY
DEFOLIATION BY GYPSY MOTH LARVAE

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INTRODUCTION

The degree and chronology of defoliation can make it an important episode in the history of a woodland. In Connecticut, for instance, the gypsy moth larvae (*Porthetria dispar*)¹ often completely strip stands at a time which coincides with the peak of vegetative activity. This deprives trees of their photosynthetic organs at the very time when days are longest. It allows light to reach lower layers in the forest at a time when they would normally be shaded. This process could harm the canopy, benefit the layers beneath it, and thereby change succession.

In the present report the canopy is represented by oak (*Quercus* sp.), which is the component of the canopy that is stripped first. The understory is represented by red maple (*Acer rubrum*) which may or may not be stripped later, depending on the demand for food by the caterpillars.

The potential benefits to red maple inherent in the food preference and timing of the caterpillars cannot be fully appreciated without understanding the normal chronology of red maple elongation. For this reason, maple elongation was studied in an open field and in two woodlands, one of which was defoliated while maple was elongating. The chronology of oak defoliation and refoliation was observed to find out how it was related to that of the elongation of maple. Finally, the effects of defoliation upon mortality and growth are presented. The belt transects investigated are described in Table I.

TABLE I. Description of six Connecticut stands. Stems smaller than 1.2 cm. dbh not measured

Plot	Location	Year of defoliation	1956-59 terminal growth studied	Seasonal elongation studied 1960	Mortality 1958-59 compared	Total area of belt transect in ha	Basal area in m ² /ha for all species	Basal area in m ² /ha for oak	Basal area in m ² /ha for red maple	Density in red maple as stems/ha
D ₁	Hamden	'57	X	X	X	.04	1.9	1.5	.2	475
D ₂	Hamden	'57	—	—	X	.04	2.4	2.0	.1	475
D ₃	Oxford	'60	—	X	—	.10	9.1	7.1	.9	230
C ₁	Hamden	—	X	—	—	.10	7.9	2.7	2.2	100
C ₂	Portland	—	—	—	X	1.32	20.0	14.0	2.7	300
C ₃	Hamden (old field)	—	—	X	—	.06	.4	—	.1	430

METHODS

1. In 1960 the normal course of red maple elongation in the field and wood was determined by periodically measuring a single uppermost twig on the largest stem of a clump. The stems were 1 to 5 m tall. I observed

¹ Insect names follow Britton (1920).

14 trees in the field (C₃), 10 in the wood (D₁) which was not defoliated in 1960, and 9 in the wood (D₃) which was defoliated in 1960.

2. In 1957 the course of defoliation and refoliation was observed in stands D₁ and D₂. The accumulated frass fall provided an objective measure of defoliation. The rain of frass during defoliation was trapped in 50 pans each 415 cm², placed at equal intervals along a 100 m transect.

In 1957 refoliation was estimated from the decrease in midday sunlight during the reappearance of the leaves. The intensity of light was measured in foot-candles with a photoelectric light meter held 1.5 m above each of the 50 pans.

3. The mortality of oak and maple was determined in defoliated (D₁ and D₂) and undefoliated (C₂) stands in the 2-yr period following defoliation in 1957. For oak, which was the large and usually dominant member of the canopy, mortality was expressed as a per cent of oak basal area. For maple, which was usually small and numerous, mortality was expressed as a per cent of maple stems.

4. Terminal elongation is another measure of plant performance that could reflect benefit or harm. Four years of elongation, identified by bud scale scars, were measured at the end of upper branches of small red maples 1 to 5 m tall in stand D₁ which was defoliated in 1957 and adjacent stand C₁ which was not defoliated because of the small amount of oak. The interference of tree-to-tree variation was minimized by expressing the annual increments as percentages of the 4-year increment for each branch, and then averaging these percentages.

This method could not be employed on oak because of the difficulty of identifying twig scars.

The formation of "lammas shoots" in red maple (Kienholz 1941) conceivably could cause confusion, but did not here for the following reasons: First, the second flushes of growth that both Kienholz and I have observed are so much smaller than the first growth that they would not be readily confused with an annual increment. Next, any second flush is less likely to occur in trees than in first and second year sprouts as observed by Kienholz. Finally, the only "lammas shoots" I have observed followed defoliation; this could not have confused the results from plots D₁ and D₂ because these maples were not defoliated and because any confusion would have produced a difference opposite to the one observed. Thus, I feel confident that relative annual twig growth properly reflected effects of defoliation.

RESULTS

1. The normal course of elongation of red maple trees free of shade is shown in Figure 1, the 1960 course for

the 14 trees growing in the open field (C_3). Compared to this the course of elongation of maples beneath a canopy of oak slowed and ceased as the canopy leafed out; thus the woodland trees ceased growing fully 6 weeks before the field-grown maples. On the other hand, maples growing beneath a defoliated canopy (D_3) were still growing two weeks after the maples beneath an undefoliated (D_1) woodland had ceased. However, the maples halted growth when they were stripped and resumed elongation until a date that coincided with the closure of the refoliated oak canopy.

Seasonal Elongation of Red Maple

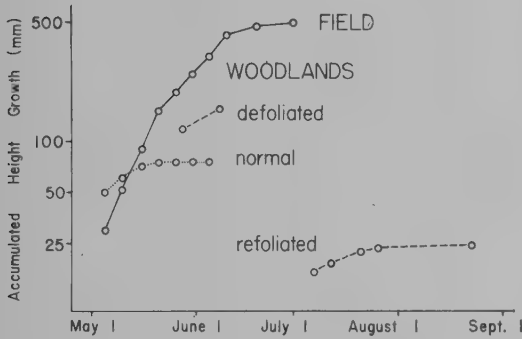


FIG. 1. Chronology of *Acer rubrum* elongation.

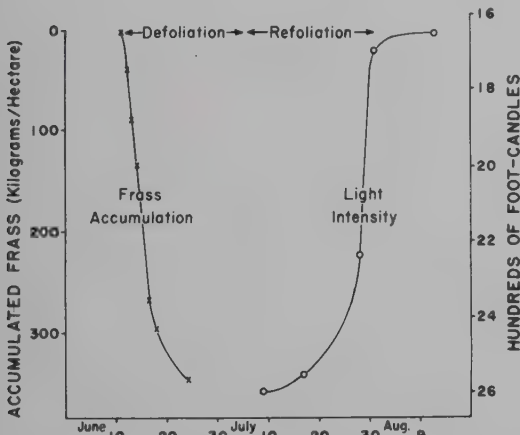


FIG. 2. Chronology of oak defoliation and refoilation.

2. That defoliation opens the oak canopy while the understory maple is still capable of elongating is shown by the chronology of defoliation and refoilation (Fig. 2). Defoliation of stand D_1 began about June 12, 1957 and the larvae stopped feeding about June 23.

During this period, 381 kgms/ha air-dry weight frass had fallen. Enough oak leaves had expanded one month later, July 20, to decrease the light intensity; by July 30, the canopy had again closed.

3. Mortality studies (Table II) in 1958 and 1959 showed that oak suffered on the defoliated plots, but red maple benefitted there. Specifically, oak losses on the

defoliated plots included dominant trees and amounted to 6% of the total oak basal area. Only 1.6% loss of oak was found on the undefoliated area, and this included no dominant trees. Red maple did not die on the defoliated plots, but underwent a 6.1% decrease in numbers on the undefoliated plot.

TABLE II. Mortality of oak and red maple on defoliated and undefoliated plots. Total area of defoliated plot (D_1 and D_2) is .08 hectares. Total area of undefoliated plot (C_2) is 1.32 hectares

	Defoliated	Undefoliated
Red maple		
No. stems	38	395
Stems per hectare	475	300
Mortality 1958-59	0%	6.1%
Oak (species listed in Table I)		
Basal area of oak and other trees per hectare	2.44 m ²	1.92 m ²
Per cent of oak only in relation to total basal area	80.0%	62.5%
Mortality of oak relative to oak basal area	6.0%	1.2%

4. Relative terminal growth of red maple in the defoliated plot (D_1) was greater in the year of defoliation, 1957, than in any other year (Table III). It was greater in the defoliated plot in 1957 than in the undefoliated in the same year.

TABLE III. Relative terminal growth of red maple, 1956-1959. Number of twigs in defoliated (D_1) and undefoliated check (C_1 and C_2) stands was 102 and 110 respectively

Stand	YEAR			
	1959	1958	1957	1956
Defoliated	22.3	23.5	27.4	26.8
Undefoliated	21.4	22.9	26.2	29.9

DISCUSSION

Two observations suggest that light intensity is the critical factor controlling elongation of maple in the woods. First, the halting of elongation in the undefoliated woodland coincided with the estimated canopy closure. Secondly, in the defoliated stand where the understory was not fully shaded, elongation continued past the normal time when it would have stopped. It did stop when refoilation occurred.

The shortened period of elongation that I observed in the undefoliated woods is similar to that reported for understory sprout oaks (Johnson 1941). While most studies of elongation have dealt with stems growing in the open under natural conditions or with seedlings growing under artificial conditions, Johnson's and my observations of short elongation periods were made in woodland shade. The contrasts in length of growing seasons for small maples between fields and woods seem best explained by light intensity. If this is true, the elongation course of trees under a canopy might prove to be a useful objective index of canopy closure.

The chronology of elongation, defoliation and refoliation leaves no doubt that maple could exploit increased light intensity.

The increased maple survival beneath oaks recently defoliated could have been due to the removal of the oak shade, to the removal of transpiring oak foliage during the 1957 drought, to the addition of nutrients in the frass or to greater photosynthesis and build up of food reserves by maple. Removing only 6% of the basal area of the oak seems insignificant. Removing transpiring oak foliage seems unimportant because the maple would at the same time transpire more. The remaining possibilities of more nutrients and reserve food seem more likely causes of decreased maple mortality.

The increased elongation of maple in the summer of oak defoliation (Table III) was not likely due to nutrients in frass because elongation was complete before the rain required to leach it had fallen. Improved water relations in the maple is also an unlikely explanation because the maple would transpire more when the oak shade was removed. Thus, increased light beneath the stripped canopy remains the most likely explanation of the increased growth.

That defoliating insects could direct succession is supported by the observation of greater mortality in the dominant oaks and greater survival in the understory maple in the years following defoliation. Although the observed increases in maple growth under defoliated oaks were small, this observation supports the hypothesis that defoliation could affect succession.

SUMMARY

1. Benefits to a plant in the understory of a stripped canopy are considered here. The plant, red maple, elongated for 2 months in the full sunlight of an old field. About a month earlier maples in the woods had ceased elongating at the same time that the overtopping oaks reached full leaf. An exception was noted in a defoliated woodland where stripping admitted light to

the maple. Here, maple continued elongation until the maple itself was defoliated; then the maple refoliated and resumed elongation until a date that coincided with the closure of the refoliated oak canopy.

2. Defoliation was measured objectively through periodic collections of frass falling into pans. Refoliation was measured objectively by a photometer held in the increasing shade of a defoliated woodland on sunny noons.

The hypothesis that light intensity controls maple elongation in the woods is supported by the chronology of elongation, defoliation and refoliation because maple elongation was synchronized to periods of high light intensity. This lengthened period of growth may be considered a benefit to maple.

3. Another benefit was the lack of maple mortality observed in defoliated stands. Since this benefit occurs over the years following defoliation, it cannot be associated with the immediate increase of light during defoliation. Nor were enough oaks killed by defoliation to increase light reaching maple significantly or permanently. However, the nutrient leached from 381 kgms/ha of air-dry frass may well contribute to the better survival of maple.

4. When annual twig growth over a four-year period was measured as the growth between leaf bud scale scars, the year of defoliation stood out as the one of greatest growth. If defoliation were frequent enough, it might favor maple in the succession process.

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TRANSPLANT EXPERIMENTS WITH CORTICOLOUS LICHENS USING A NEW TECHNIQUE¹

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The many studies on the autecology of lichens have been thoroughly reviewed by Barkman (1958). With few exceptions, these studies were based on field observations and were primarily descriptive. From these

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²The author wishes to sincerely thank Dr. Eugene C. Ogden and Mr. Herbert Mapes of the New York State Museum for their suggestions and aid during the summer, and Drs. John Cantlon and Henry A. Imshaug for their help in the preparation of the manuscript. A debt of gratitude is owed Mr. Harold P. McManus, Queens Borough Director of the New York Department of Parks, for granting permission to carry out the necessary transplant work in the city parks.

methods much is learned about ecological factors governing the distribution of lichens, but controlled experiments in the field or laboratory are necessary to separate the large number of factors involved. The lack of such experimentation is mainly due to the slow growth of lichen thalli. A few transplant programs were carried out using ground-dwelling lichens (Hale 1950, 1954, 1959; Lindahl 1953), and some other studies were made on nitrogen relations in *Peltigera polydactyla* (Neck.) Hoffm. (Smith 1960). The ecology of corticolous lichens has rarely been studied experimentally probably because of the susceptibility of such thalli to damage in removal from their substrate, and the impractical nature of moving the substrate with its associated lichen thallus. A transplantation was carried out by Henry Imshaug, Clifford Wetmore and myself in 1959. A number of twig lichens characteristic of the northern Michigan pine barrens were transferred on dead branches

from northern Michigan to a bog near Lansing, Mich. Thomson (in press) reported that a new lichen distribution was established in California by the successful though accidental transplantation of an eastern *Physcia* on an ornamental tree introduced from eastern U.S.

My study of the ecology of lichens of Long Island, N.Y., indicated that a controlled experimental technique was needed to clarify the factors influencing the distribution and ecology of some corticolous lichens. Dr. John Cantlon and I devised a technique to transplant corticolous lichens by lichen-bearing bark disks.

PROCEDURE

The transplant procedure involved removing a lichen with its substrate as a bark disk and transplanting it intact. The death of the inner bark tissues of the disk presumably has little effect on the attached lichens, which commonly grow on dead as well as living trees.

The "bark-borer" used was designed and built by Mr. Herbert Mapes of the New York State Museum staff, and myself. It consists of a hole-saw blade beveled on the outside to a sharp cutting edge, and a holder. The latter is a single piece of steel, the large end holding the blade and the smaller serving as a handle which can be hammered to drive the blade into the bark (Fig. 1). To

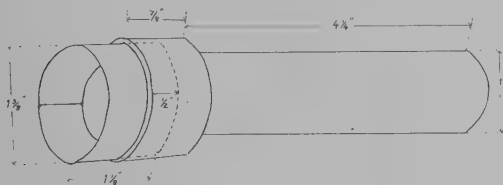


FIG. 1. Sketch of "bark-borer". The cylindrical blade (at the left) is recessed $\frac{1}{2}$ in. into the expanded portion of the steel holder. The beveling of the blade edge is not shown.

collect the bark disk, the instrument is placed against the bark and the blade hammered in about $\frac{1}{2}$ – $\frac{3}{4}$ inch. The disk is loosened by gently hitting the sides of the handle with the palm of the hand. If the borer is driven in evenly and the inner bark is loose, the bark disk separates from the inner bark and is removed with the borer. To remove the disk from the borer without damaging the lichen, the blade is removed from the holder. Upon removal, the blade spreads slightly and releases the disk. If the disk does not detach from the tree with the borer, it can be freed by carefully chiseling around the edge of the disk and prying it loose.

After the disks were removed, the holes in the trees were scraped clean and flat. The disks were numbered, placed in envelopes, taken to the laboratory, and photographed (Fig. 2). The uniform diameter of the disks ($1\frac{1}{2}$ in.) provided a scale for the photographs.

For the transplantation each disk was fastened into its new position in a second hole made as described above in the same or another tree. Grafting wax (a mixture of linseed oil and bee's wax) was used as an adhesive since it is easy to handle, easy to obtain, and contains no known toxic volatile substances. For the wax to be effective, the transfer hole and disk surfaces had to be fairly smooth and dry. If the disk was too thick for the hole, the inside surface of the disk was trimmed to fit. The back of the disk was then covered with a generous quantity of grafting wax and the disk was pushed into the hole. The slight shrinkage of the disk since the time of its removal provided just enough



FIG. 2. Bark disk bearing *Parmelia caperata*. The disk is $1\frac{1}{2}$ in. in diameter.

extra space to accommodate the wax and maintain a snug fit. After some time the linseed oil oxidized, thus hardening the wax.

EXPERIMENTS PERFORMED

Vertical Distribution

Many corticolous cryptogams are known to have a specific vertical distribution on trees (Barkman 1958). Some species are base-dwelling and others grow only above the basal region. Factors which may be involved in this vertical distribution are light, moisture, age of bark, texture of bark, and presence or absence of accumulated organic matter on the bark surface. Transplant experiments involving the transfer of lichen-bearing disks from one height to another were designed to study some of these factors.

Sets of 3 bark disks were removed from 20 trees and each disk numbered. The disks in each set were selected so that their associated lichens originated from the same thallus, or, if this was impossible, from adjacent thalli.

The first disk was placed in a new vertical position on the same side of the same tree. A compass was used to ensure an exact duplication of the original exposure. Disks from the basal region were transferred to a height of 1.3 m; disks taken from breast height were repositioned at a height of 6 cm. The other 2 disks were controls, the second being placed in the hole left by the first and therefore remaining close to its original position although in a new hole. The third disk was replaced in its own hole using wax. From disk 2 the possible influence of a discontinuity of the cambium layers could be studied, and from 3, the influence of removal and replacement techniques could be noted.

A base-dwelling species, *Cladonia chlorophaea* (Floerke) Spreng., and a species usually found at breast height, *Lecanora leptyroides* (Nyl.) Nilss.,³ were used.

³The Long Island material referred to as *Lecanora leptyroides* is not conspecific with the European *L. leptyroides*. The name is retained, however, until a study of the *L. pallida* group in North America has been completed.

The trees were *Quercus velutina* Lam. and were in a homogeneous young oak woods near the 100 ft meteorology tower at Brookhaven National Laboratory, Upton, Long Island, N.Y. (Fig. 3). Ten sets of 3 disks each were set up for each of the 2 lichens. Thus, a total of 20 trees and 60 bark disks were used.

LONG ISLAND, N.Y.

• EAST-WEST TRANSPLANT LOCALITIES

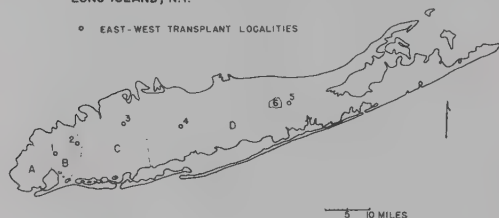


FIG. 3. Long Island, New York. A. Brooklyn (New York City), B. Queens (N.Y.C.), C. Nassau County, D. Suffolk County; 1. Forest Park, 2. Alley Pond Park, 3. Brookville, 4. Commack, 5. Manorville, 6. Brookhaven National Laboratory, Upton.

Bark disks were examined in December, 1961, 4 months after transplantation. Over half of the vertically repositioned thalli of *Cladonia chlorophaea* showed signs of death and every control thallus of this species appeared healthy (Table I).

TABLE I. Vertical Transplants: The condition of the transplanted thalli of *Cladonia chlorophaea* (a fruticose lichen) four months after transplantation. +++ = healthy; ++ = some damage; + = almost completely destroyed; 0 = completely destroyed

Tree number	TRANS. DISK	CONTROL DISKS	
	1	2	3
K.....	+++	+++	+++
L.....	0	+++	+++
M.....	++	+++	+++
N.....	++	+++	+++
O.....	++	+++	+++
P.....	+++	+++	+++
Q.....	++	+++	+++
R.....	+++	+++	+++
S.....	+++	+++	+++
T.....	+	+++	+++

Thus, the restriction of *Cladonia chlorophaea* to a basal habitat appears to be due at least partly to microclimatic factors, the most important of which is probably moisture. If the bark composition or texture or accumulated organic matter on the base were the sole determinants, no death would have occurred merely by changing the position of the substrate. Bark characters may be important in the establishment and survival of *C. chlorophaea*, but these results indicate that a suitable microclimate is essential for survival. No conclusions are drawn from observations of *Lecanora leptyroides* because of extensive exudation damage which the lichen suffered.

East-West Distribution

A similar experiment was set up to examine the effects of the New York City environment on the east-west distribution of lichens. Approaching a large

town or city, one can see a gradual reduction in abundance of lichens (Rydzak 1959, Fenton 1960, Jones 1952, Magdefrau 1960). By transplanting bark disks from eastern Long Island to areas at various distances from the city, the rapidity and severity of lichen damage can be studied in relation to these distances.

Fifty disks were removed from mature oak trees near Manorville, Long Island. *Lecanora leptyroides*, a crustose species, was on 25 disks removed from scarlet oaks (*Quercus coccinea* Muenchh.); *Parmelia caperata* (L.) Ach., a foliose lichen, was on 25 disks taken from black oaks (*Quercus velutina*).

Five disks of each species were placed in each of the following localities: in their original positions at Manorville (56 miles east of Forest Park in New York City), Commack (30 miles east of Forest Park), Brookville (16 miles east of Forest Park), Alley Pond Park (at the eastern edge of Queens County and 6.5 miles east of Forest Park), and Forest Park (Fig. 3).

The trees in the new locations were the same as the original substrates with the exception of Alley Pond and Forest Parks where red oaks (*Quercus rubra* L.) were used. Height and exposure were identical with the original. Trees were selected to duplicate the original conditions of light and humidity as closely as possible.

TABLE II. East-West Transplants: The condition of the transplanted thalli of *Parmelia caperata* (a foliose lichen) 4 months after transplantation. The symbols are the same as in Table I

Location	PARMELIA CAPERATA				
	DISK NUMBERS				
	1	2	3	4	5
Manorville.....	+++	++	+++	++	++
Commack.....	++	+++	+++	++	+++
Brookville.....	++	+	++	++	++
Alley Pond Pk.....	++	+	++	+	0
Forest Park.....	+	+	++	+	+

Parmelia caperata showed a definite increase in thallus damage from east to west (Table II). Most of the damaged thalli of *Lecanora leptyroides* were covered to varying degrees with exudations from the surrounding cuts and therefore, no conclusions can be drawn from their condition.

Apparently New York City has a strong detrimental effect on lichen growth and survival. The cause of this effect has not yet been ascertained. Moisture relations (Rydzak 1959) and atmospheric pollution (Fenton 1960, Jones 1952, Magdefrau 1960) have been suggested as possible explanations of the influence of towns on lichen growth. Plans are being made by the author to set up a transplant experiment on Long Island to study these factors. Since the effects of transplanting appear quickly and can easily be seen and analyzed, lichens may be noteworthy as natural indicators of air pollution.

GENERAL RESULTS AND CONCLUSIONS

Only one of 110 disks removed and replaced fell out of its new position and this was probably due to insufficient adhesive. Most of the repositioned thalli showed clear evidence of some damage whereas the controls, except for the exudate-damaged *Lecanora leptyroides*, were essentially unaffected.

The different lichens were damaged in different ways, but apparently most were manifestations of the death and decolorization of the algal layer. *Parmelia caperata* turned yellow and then white. *Lecanora leptyroides* showed a decolorization of the grey thallus, and the normally lavender apothecia turned white and shriveled. The podetia and basal squamules of *Cladonia chlorophaea* became pale and then shriveled.

Generally, crustose lichens appear to be inferior to macrolichens as ecological indicators on transplanted disks. This is due to the nature of a closely adnate crustose thallus and its susceptibility to surface damage by bark exudations. However, it may be possible to eliminate this type of damage by covering all cut surfaces with small amounts of grafting wax, or by using a more effective seal.

The transplant technique, including cutting the lichen thallus and killing the substrate, has no noticeable effect on the lichen except for the exudation damage noted with the crustose thalli. This technique may therefore be useful in problems involving controlled experimentation with lichens. This is particularly important in the study of lichen ecology and physiology since no other technique involving the transplantation of corticolous lichens is available.

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SOME OBSERVATIONS ON BALD CYPRESS IN INDIANA

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There has been considerable speculation regarding the formation of the "knees" on bald cypress (*Taxodium distichum*). While it is not the purpose of this article to explain the formation of "knees," cypress records in Indiana taken during the past 30 years may help explain their development.

Many authors and observers have speculated about the possible functions of the "knees." Early writers believed that they were organs useful in permitting gas exchange for the submerged roots (Wells 1942). However, much evidence has been assembled against this theory. Kramer, Riley and Bannister (1952) measured the gas exchange between the "knees" and the root system on which they occur and found it to be minutely small. The gas exchange they found in their experiments was so small it is likely that it was merely due to experimental error. An unpublished experiment of Penfound in 1934 (described by Kramer, Riley and Bannister) showed that the removal of the "knees" from the roots had little if any effect on the growth of the tree.

Mattoon (1915) credits Lamborn and many other observers who thought that the primary function of the "knees" is to stiffen and strengthen the roots in order

that the tree may be firmly anchored in the yielding medium.

The "knees" frequently form in a ring about the base of the tree. They are more numerous and larger and the root systems are correspondingly more extensive on trees growing where the ground is the most spongy and soft. Each "knee" has its own individual root system which is smaller but very similar in appearance to the main root system beneath the tree.

The "knees" and buttresses form only where air and water act together on the wood-forming tissues, so generally trees growing either on permanently dry land or permanently submerged land do not develop "knees" or swollen bases, according to Kurz and Demaree (1934). As a rule "knees" which develop in shallow water which does not fluctuate excessively are low and wide. Those which develop in water which fluctuates many feet are narrow and conical. "Knees" as tall as eight to ten feet above the water line have been observed. Usually the height of the "knees" closely corresponds to the normal high water level of the site.

Bald cypress has been planted in various parts of Indiana during the past 30 to 40 years. It has been planted on a wide variety of sites ranging from sand hills to swampy areas.

¹Deceased, September 21, 1961.

One of the most interesting plantations was started in 1929 when one-year seedlings were planted for a wind-break in Northeastern Indiana.² A single row planting consisting of 100 trees was set out on both muck soil and sandy loam. A picture (Fig. 1) taken of the trees in 1932 illustrates early growth of the cypress. The trees were kept free of weeds and in 1936 70 trees remained;

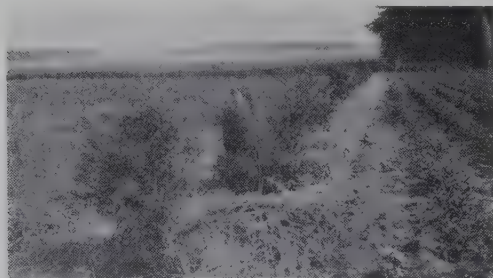


FIG. 1. Cypress planted on muck soil and sandy loam in 1929. Photo taken in 1932 shows trees well established. Trees varied from 2 to 5 ft in total height.



FIG. 2. Twenty-five years after planting, these cypress were from 12 to 18 inches in diameter and 25 to 35 feet in total height.



FIG. 3. The 25 year old cypress had well developed knees. Trees growing on sandy loam and muck soil.

the largest had attained 3 in. dbh and a height of 12 ft. By 1950 the maximum diameter attained was 16 in. and

² Editor's note.—The northernmost site for bald cypress as it occurs naturally in Indiana is in Little Cypress Swamp, Southwestern Knox County, in extreme southwestern Indiana.

at that time cypress "knees" had developed on some of the trees. By 1954 or 25 years after planting the cypress ranged from 25 to 35 ft in height and 12-18 in. dbh (Fig. 2). Trees on both the muck soil and sandy loam had well developed knees (Fig. 3). Water action could not account for the formation of "knees" on this site. The area is used for crops and is artificially drained. The site is a moist one but not covered with water for more than a few hours during heavy precipitation.

In Owen County, which is located in south central Indiana, a planting was made in 1939 on an eroded field, the soil a Parke silt loam. Red, white, short leaf pine and black locust were planted. However, on small areas several groups of from 25 to 50 bald cypress were planted in small coves which were the more moist sites. Five years after planting, the seedlings had attained 1.5 in. dbh and were 15 ft tall. Each year the trees were examined to see if "knees" were developing. In 1951 or 12 years after planting, "knees" were visible on 10% of the trees. Photos taken in 1954 (Fig. 4) show the "knees" and since that time annual inspection of the trees showed continued growth of "knees."

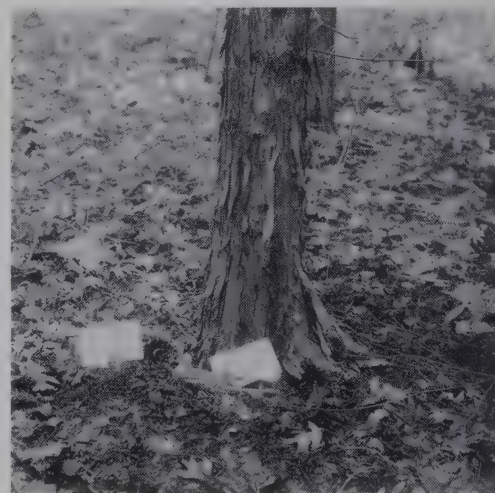


FIG. 4. Cypress planted on Parke silt loam soil in 1939 had knees in 1951, 12 years after planting. Photo taken in 1954 shows knees which have developed close to base of tree.

The only water action occurs during periods of excessive precipitation, and water will remain in these coves for only a day or two.

In 1939 one-year old bald cypress were planted on a pin oak flat along a small creek in Noble County in northeastern Indiana; open places where there was room for 20 to 25 trees in a spot were chosen. Although survival of cypress was only 10 percent, those trees that did survive attained a maximum dbh of 6 in. and a height of 30 ft 20 years after planting. The "knees" on the root systems at this time were 2-4 in. in height and averaged 3 per root system.

Observations were made annually and "knees" were found when the trees were 15 yrs. old. On this site the creek seldom overflows and only during periods of heavy precipitation does this occur. Water action of

such short duration cannot account for formation of the "knees."

All three of these examples illustrate that cypress "knees" do develop on trees planted on various sites outside of their natural range in Indiana.

It is my conclusion that the development of cypress "knees" is an inherent characteristic of the species.

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THE LIFE CYCLE OF *HELENIUM AMARUM*

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Helenium amarum (Raf.) H. Rock (*H. tenuifolium* Nutt.) is a common pasture pest of the southeastern U. S. Its U. S. range extends from Texas (Small 1933) eastward to the Atlantic Ocean, and northward from the Gulf of Mexico into southeastern Indiana (Deam 1940), southern Illinois (Mohlenbrock and Voigt 1959), and central Missouri (Steyermark 1959). It reportedly grows as far north as Massachusetts, New York, Ohio, and Michigan (Fernald 1950); as far southeast as Cuba (Rydberg 1932); and as far southwest as Sonora, Mexico (Torrey 1859). It has recently become established in at least 2 places in California (Munz 1959, Abrams and Ferris 1960). The species is commonly called bitterweed where it grows abundantly because of a bitter principle (Shields 1952) in the leaves and stems. This imparts a disagreeable flavor to milk and milk products from cows which have eaten it. It is much despised by farmers and has long been given attention in programs of weed control in the southeast (Piper and Carrier 1920).

H. amarum is generally considered an annual plant (Fernald 1950, Abrams and Ferris 1960). Harper (1936) stated that in the early spring it has a rosette of leaves which wither before the plant blooms. He probably did not consider it a winter annual, for he did not list it among the common winter annuals of the Tuscaloosa, Ala. area (Harper 1958). Mohr (1901) termed it a perennial.

Preliminary experiments dealing with germination of the seeds of this weed indicated that there was no natural dormancy under greenhouse conditions at the University of Chicago. Freshly collected seeds germinated there within 3 or 4 days when placed on sand and kept moist. It was, therefore, believed that the seeds would not lie dormant through the winter in southern pastures. Subsequent field investigations in Tennessee, Mississippi, and Louisiana indicated that the seeds germinate in the early fall. The plants then overwinter as small rosettes and bolt in the spring. The appearance of these rosettes is shown in Figure 1. Near Jackson, Miss., small rosettes were found as early as Sept. 27. In the same area bolting occurred during the first 2 weeks of April. The rosettes grow slowly; the mean diameter of 100 plants measured in a pasture near Jackson on Feb. 8, 1960, was 30.5 ± 0.8 mm. Additional studies, as yet unpublished, indicate that the time of bolting and flowering is controlled by the length of the photoperiod. Flowering begins in central Mississippi about June 1.



FIG. 1. The general appearance of the rosettes of *H. amarum*. These plants were grown in a Chicago greenhouse, but are generally quite similar to the winter form in the Southeast.

H. amarum is, therefore, a winter annual. Recognition of this fact is imperative in future study of its ecologic relationships and in the planning of weed-control programs where it is involved. It explains immediately, for instance, why this weed is not present in fields which are cultivated in the fall or early spring. It also indicates that the critical periods of competition between this species and associated plants may be fall, winter, and early spring, rather than summer.

The author is especially indebted to R. P. Ward, Wayne McIlrath, and W. N. Rushing for aid and criticism. A portion of the work was completed while the author held a National Science Foundation Science Faculty Fellowship at the Univ. of Chicago.

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REVIEWS

WILDLIFE IN AN AFRICAN TERRITORY¹

The investigation here reported was undertaken on the invitation of the Director of the Game and Tsetse Control Department of Northern Rhodesia. The field work was done in a six month's period—February to April, and August to October, 1956, and July to October, 1957. As all who are acquainted with him know, Dr. Darling is not one to take at second hand information about the ecology of an area with which he is concerned. The lands traversed were extensive, as shown by an insert map—but Dr. Darling makes no mention of the discomforts, difficulties and dangers encountered in getting the job done. Means of transportation were various, including aeroplane, launch, automobile, and dugout canoe, as well as wading (probably also some swimming!), and extensive hiking on foot.

According to Darling, Northern Rhodesia still possesses some of the finest faunal areas in Africa. "The question is, are these to be conserved or let disappear: and the problem is, assuming the answer to be care of habitat and animals, how can management and good husbandry be achieved?" (p. v.)

Obviously the pains associated with the birth of a number of new African nations affect not only the human population, but also the wildlife. Indeed, in some respects, the far-reaching changes taking place may rest more heavily on the vegetation and wild animals than on man. Mention is made (p. 79) of Darling's receipt of a letter from an old friend, the late Dr. Homer Leroy Shantz of Santa Barbara, California (formerly of the University of Arizona and the United States Department of Agriculture) who, with Dr. Marbut, made the first vegetation map of Africa in 1923. Retracing his steps thirty-five years later Dr. Shantz was dismayed at the deterioration which had taken place.

The present study is a convincing demonstration of the value and indeed necessity of an ecological approach to wildlife and habitat management. Unfortunately "... the opportunist, profit-seeking, so-called practical approach to apportionment of land use ... is still common. Growing understanding of ecological principles raises the conservation of nature to an ethic, the precept of which is that the eternal must not be sacrificed to the expedient." (p. 5.)

As in so many other places, here also the central problem is one in human ecology. Evidently human population pressure is placing a heavier strain on all the resources. Although mentioned incidentally in several places in the book, the vital significance of human population increase is not as sharply emphasized as it should be. It is true that Dr. Darling mentions the three-fold increase of human population of Northern Rhodesia in the last sixty years, while the wild ungulates "... have been depleted to a fraction which cannot be estimated. ..." (p. 4.) Says the author, "The Pax Britannica is bound up with saving lives by all manner of hygienic and prophylactic measures, usually without reference to the consequences, because until a slightly disillusioned present, the notion of progress was taken to be lineal and certain and, of course, the notion of a constantly

expanding economy went with it. The human ecologist, a sour fellow perhaps, sees the sudden eruption of the present ill-phased situation as one more example of raising the numbers of a population at the expense of their diets. The picture is one of bicycles, carbohydrates, and sedition as against the greater content of fewer people receiving adequate protein." (p. 98.) It is coming to be realized by more and more biologists that in the absence of some effective form of regulation of human population all other efforts for sane conservation of wildlife and other natural resources anywhere in the world are doomed, at last, to failure.

By no means all the wildlife and habitat depletion is chargeable to the native. "... the processes of destruction have accelerated since the advent of the white man. Sometimes he seems to have gone berserk and far exceeded the Bantu in actions of direct and positive destruction. ..." The toll of wildlife taken by the rural African might be made up for, Darling thinks, if the animals were taken purely for family consumption, and if, at the same time, the habitat were not modified for the worse. Unfortunately, commercialism, through the "insatiable meat hunger of the Copper Belt" is a real and serious threat.

Not as yet appreciated by the African is the tourist value of wildlife. It is to be hoped that the International Union for the Conservation of Nature and other world and national conservation agencies, as well as local administrators, may succeed in their efforts to inform the native and motivate him to conserve the wildlife, often one of his potentially most remunerative assets. Here, again, is a sort of race between education and catastrophe.

A forthright discussion is included of the relative value of the wild native ungulates and the imported domesticated live stock. The author points out that "The stratification of the uniquely wide spectrum or array of African hoofed animals ... contrasted with the very narrow spectrum of three domesticated animals ... makes much fuller usage of habitat without deteriorating it. In general, pastoralism of wild lands by cattle, sheep, and goats causes gross deterioration of habitat. ... The thesis is put forward that a cropping policy of the wild ungulate animals, including elephants, will give a higher and a more continuous protein offtake than pastoralism of wild land." (pp. 130-131.) Other authors (cf. E. B. Worthington, *ORYX*, vol. 5, no. 6, p. 344, Nov. 1960, and R. F. Dasmann and A. S. Mossman, *RHODESIAN FARMER*, April 15, 1960) also have suggested the more favorable cash value and production which may be expected from the native ungulates as compared with imported domesticated breeds. A convincing basis for these conclusions is afforded by the tabulation (pp. 91-93) of the variety of ecological requirements of the various African ungulates. Many will agree with Darling's conclusion that "... to exchange the wide spectrum of African ungulates living in delicate adjustment to the poor and tender habitat for the narrowed spectrum of three ungulates exotic to Africa—cattle, sheep, and goats—is to throw away a bountiful natural resource and a marvelous ordering of nature." (p. 95.)

The use of fire is a problem in Africa, much as in our own continent. Says the author, Fire "... is a tool of despair and its practice results in direct impoverish-

¹ Darling, F. Fraser. 1960. *Wild life in an African territory; a study made for the Game and Tsetse Control Department of Northern Rhodesia*. Oxford University Press, London, New York, Toronto. x + 160 pp., colored frontispiece, 3 maps. \$4.00.

ment of the range." (p. 85) Some of the effects of man-made fires (p. 83) remind one of our own American wildlands. As a result of fire: forests have become savannah, savannah has become total grassland, grassland has become desert or has been invaded by thorn bush and tsetse fly.

As might be expected in the vast array of wild species and environmental conditions, there are numerous extremely interesting instances of interrelationships. Some of these are associated with the elephant, which is so successful in exploiting its environment that, unlike most of the African fauna, the species tends toward overpopulation. One example of elephant interrelations concerns the funnel-shaped trunk holes dug in the sand to reach water (p. 21). Dependent, sometimes, on these water sources are the rhinoceros, baboons, francolins, guinea fowl and doves. When the elephants moved out, many rhinoceros died. (p. 22.) A small fish makes its nest in the cylindrical trough created on the floor of a lagoon by the elephant's foot. (p. 90.)

In view of the possible far-reaching effects of the lion and other carnivores on the ungulate populations it is to be regretted that more attention was not given to them. This shortcoming however, may not be charge-

able to the author, as editors and publishers are sometimes notoriously arbitrary in excising important material.

Without further documentation and figures, one may doubt that "An ecological climax represents the maximum energy flux in any set of physical and climatic conditions." (p. 93.) In the North American Continent, at least, seral stages, some of them, are far more productive, e.g., of game animals, than is the climax. More study is needed on this point.

This book is a thoughtful and valuable contribution not only to the solution of a series of problems in local biological administration but to statesmanlike management of natural resources widely over the earth. Every page provides food for thought. The volume communicates with much success the earnest and well-considered views and conclusions of one of the keenest and clearest-headed of the world's living ecologists. It is to be hoped that officials and citizens interested in any phase of resource management may read and profit by it.

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THE WILDLIFE OF MEXICO¹

Here, at last, is a book on the wildlife of our all-too-little known neighbor on the South. Almost every page includes ecological material of interest and value. The author credits William Vogt, former Head of the Conservation Section of the Pan American Union, with raising the money to get the undertaking started and directing its formative years. The foreword is by Enrique Beltran, undoubtedly the ablest living Mexican conservationist.

As would be anticipated from the long-standing tradition of excellence built up by the University of California Press, the book is well bound and typographically attractive. The reviewer found but one misspelled word in the entire volume (on page 381, *gooddingii*, a species of willow, instead of *gooddingii*). Furthermore the work is beautifully illustrated. For each principal species there is usually a full page devoted to black and white line drawings by Charles W. Schwartz. Included on each is a sketch of the bird or mammal in its habitat, its characteristic or diagnostic features, and a map of its distribution in Mexico. The grizzly bear and ocelot are illustrated by colored plates. There are also a number of exceptionally fine animal portraits, by Paul J. Fair and Schwartz.

Whether to sportsman, wildlife manager, or naturalist, on this side of the border, Leopold's book cannot fail to be absorbingly interesting, since it treats among others, such novelties, to the North American, as the tinamous, curassows, guans, chachalacas, Douglas quail, and ocellated turkey among birds, and the spider and howler monkeys, tapirs, volcano rabbit, Deppe squirrel, coati, kinkajou, tayra, grison, jaguar, and brocket deer among mammals.

¹ Leopold, A. Starker. 1959. *Wildlife of Mexico*; the game birds and mammals. University of California Press, Berkeley and Los Angeles; Cambridge University Press, London. xvi + 568 pp., 194 figs., 18 tables. \$12.50.

In handling the geographic distribution of Mexican wildlife the author follows the biotic community concept of various writers, instead of the life zone system of Dr. C. Hart Merriam.

Leopold points out that problems of human population underlie all the woes of game conservation in Mexico. Here, as elsewhere, "Conservation of game is dependent first and foremost upon conservation of game environment—the land, the vegetation, and the water." (p. 44.) The "Waste Makers" have been industrious in Mexico as in other parts of the world. Logging of forested areas, even when conducted under government supervision, has been wasteful and destructive, "... since the only objective is immediate profit."

The ecologist cannot help but be impressed with the need, all over Mexico, for the regulation of livestock grazing, as well as of other forms of potentially destructive exploitation. The problem of getting control of domestic livestock, especially sheep and goats, appears to be almost as difficult in Mexico as it has proven to be in Spain, Greece, Turkey, and other Near East and Mediterranean countries.

Leopold corrects an impression which unfortunately has been expressed by many American sportsmen, namely, that the decrease in our waterfowl has been due to illegal shooting by Mexicans. He points out that the total annual take of waterfowl in Mexico is less than American hunters shoot in an average weekend during the season.

The author's dropping of the possessive "s" in vernacular names of birds is refreshing. *Lophortyx gambeli* is no more Gambel's quail than the famous national park in the State of Washington is Rainier's Park.

Depending on their ecological predilections the different Mexican quails respond differently to civilization. For example, there is no problem of conservation with the Douglas quail (p. 242) which lives in cutover forest

lands, or with the Yucatan bobwhite, which thrives in a farm environment; but the masked bobwhite of Sonora (and formerly of southern Arizona) is en route to extinction because of overgrazing of its river bottom and foothill ranges (p. 250). Similarly the spotted wood quail of the wet tropical forests disappears when the forest canopy is broken and a brushy understory springs up. (p. 255.) Leopold has made it clear that there is hardly a phase of wildlife distribution and management which is not in essence profoundly ecological.

The readers should not miss the accounts of the deer, javelinas, brockets, bighorn sheep and pronghorns. Survival of the brocket depends on saving enough tropical forest to take care of it. Bighorns are peculiarly vulnerable to hunting. Antelopes also are not well-adapted

to avoid the highpower rifles of today's hunters. It is possible that competition with domestic stock for range forage is even more serious to their future.

If this book can be made available to community leaders in Mexico and acted upon, a new day in wildlife conservation and management in that great country may well be ahead. It will be necessary, however, to re-establish courses in the schools of the type of Beltran's "Wildlife Zoology" and to spend at least some money, thought, and energy in educating the general public and enforcing the game laws. In this book Leopold has made a major contribution to the future.

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THE HUMAN USE OF THE EARTH¹

It is a familiar rule of experience among ecologists that the relation of any species to its natural environment is mediated by its behaviour pattern. It is a further rule of experience that as living communities develop, they play an increasing part in influencing the character of the environment they occupy. Extending these concepts to man, we have the now well-understood principle that human societies interrelate with the natural environment through the patterns of their cultures and the unquestionable fact that the cultural environment continues to play an increasingly powerful role.

Professor Wagner of the Department of Geography of the University of Chicago devotes his volume to the detailed exposition of these ideas so far as man is concerned, drawing upon an obviously wide range of reading and experience. So doing he moves from a consideration of man's place in nature to discuss his cultures, their distribution, economics, operation and effects in creating what he calls an artificial environment.

His presentation is threaded with a running sequence of terms, conveniently italicized and defined as they

appear. Many of these terms are already so well-standardized in literate usage that the informed reader is likely to be puzzled at times, uncertain as to whether he is wading into a closely reasoned theorem or a suite of variations on familiar themes. This is not to imply that there are not passages of reflective analysis and a considerable amount of useful information which has needed assembling. Certainly the body of knowledge presented ought to be part of the equipment of the educated citizen of today.

The author presents, at the end, 15 propositions, under the heading of Conclusions and Observations, emphasizing the artificiality of the human environment and its steadily increasing role in human affairs and in modification of the natural environment. While recognizing the existence of natural, societal and technical limitations, he seems to me to imply a strongly stabilizing effect to the growingly interdependent artificial environment of mankind. Properly, but perhaps too briefly, he notes its vulnerability, so clearly emphasized by Samuel Perkins Marsh nearly a century ago.

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¹ Wagner, Philip L. 1960. *The human use of the earth*. The Free Press of Glencoe, Illinois. xv + 270 pp., 7 figs. \$6.00.

THE SALT-MARSH ECOSYSTEM¹

Few ecologists have had the courage to undertake the description of an entire major ecosystem on a world-wide scale. Even fewer have succeeded in bringing such a description, in any great detail, to the stage of publication. The present book firmly establishes Professor Chapman in this elite.

This is not a mere summary, but a detailed account. It is based, of course, largely on the available published

work, but this is amplified and given substance, to a very great degree, by the author's field experience. His own papers on salt-marshes fill almost a full page of the 19-page bibliography and he has personally studied many of the principal salt-marsh areas of the world.

Probably most readers would without hesitation, refer to this book as a study of vegetation. The author clearly thinks of it as more than that, though he nowhere explains whether he regards the salt-marsh as a geographical feature, a type of landscape, or an ecosystem. The fact that he goes into the chemical nature of the site, the dynamics of the vegetation, and the physiology of the plants makes it clear that he is treating the

¹ Chapman, V. J. 1960. *Salt marshes and salt deserts of the world*, Leonard Hill (Books) Ltd., London; Interscience Publishers, Inc. New York (Plant Science Monographs, ed. by Nicholas Polunin). xvi + 392 pp., 102 figs., 45 plates, 52 tables. \$14.50.

subject much more intensively and ecologically than would a geographer. The study is definitely an ecological one. But in no way does it follow the scheme of most modern studies of ecosystems, which attempt to construct theoretical models usually illustrating the patterns of flow of matter and energy through open systems. The Chapman volume is strictly a description of the physical and biological features of, and the chemical and ecological processes going on in, a well-defined segment of the natural world. As such it is clearly a kind of description of an ecosystem, much more along classical than ultra-modern lines. Productivity, though mentioned appropriately here and there, is not in any sense either the catch-word or the central theme. Therefore the factual information is expressed in terms of percent and fractions of percent rather than in orders of magnitude. While in no sense wishing to detract from the value of carefully done productivity studies and sound energy-flow models, the reviewer is glad to use this book as an example showing that ecological work, to be of real value and significance, need not, even now, conform to any one fashion or pattern.

The book, very soundly, starts with a brief statement of what salt-marshes are and where they occur, a characterization of the vegetation, and a declaration of the obvious fact that the vegetation is seral in character.

Then follow a physiographic description, with due attention to sedimentation processes and their importance, a consideration of the hydrology, and a detailed discussion of saline and alkaline soils and their ecology.

Chapters V to IX are a detailed survey of the salt-marshes and salt deserts of the world, with a quite disproportionate amount of attention given to British salt-marshes. This is, of course, partly due to the author's own experience, but probably also reflects more available published work on these British marshes than on those of any other region. In these chapters it is increasingly evident that the salt desert part of the book was included because of an unescapable similarity of these areas to salt-marshes rather than from any great interest in or understanding of them on the part of the author. The book would have been a much more coherent unit if no attempt had been made to deal with the salt deserts (as distinct from the inland salt-marshes), as they are given slight and inadequate attention indeed.

It is in this section, too, that the other important defect of the book becomes evident. Clearly the author does not know what to do about the related questions of classification and terminology of salt-marsh vegetation. In an attempt to retain the advantages of Anglo-American descriptive terminology and at the same time, apparently, to woo the continental readers with terminology of a form familiar to them, he has produced a confusion fully justifying those who will use this book as another horrible example of the morass of ecological language. He will certainly please neither group of readers. Although in some examples where phytosociological designations are used, the units are those established by

phytosociological procedures, in a great many others it only appears so, and the names are merely a reflection of what are the dominant plants. And to find (p. 252) the terms "General Salt-Marsh," "*Salicornia mucronata*," and "*Spartinetum patensis*," applied to communities in the same diagram is incongruous. Another defect in the organization of the book is the extensive use of special terminology before any attempt is made to explain it. The grouping of the rather mistitled, and not very successful, "Salt-marsh Survey," an attempt to establish degree of relationship between the marshes of different regions, in the same chapter with the fascinating discussion of the "Salt-Marsh Fucoids" is also a curious arrangement.

Throughout the book, except in the last two chapters, the interpretation is in terms of succession, and even the last chapter is fundamentally based on this viewpoint. Diagrams are introduced to help the reader visualize the complex successional relationships wherever the available information justifies it. These successional patterns are closely related to, and dependent on, physiographic processes, especially sedimentation, sea level change, and erosion. This part of the book is generally convincing and, where the information is adequate, seems sound.

The chapter on the physiology of halophytes brings together a vast amount of data and attempts some generalization. It is clear that before real consistency emerges in this autecological field much more work will be necessary. However, there is a real danger that this work will smother itself in a morass of detail and will be slow in bringing principles to light. Periodic reviews, such as this chapter, will be essential to keep the field in order.

The final chapter, on Economic Uses, contains much material of interest, but is much less thorough than the others—probably because to be that thorough would have doubled the size of the book. It is traditional that such a chapter or section be included in ecology texts, but generally, as here, it would be better either to omit it or to frame it more in terms of human ecology than in those of economics or economic geography.

At the beginning of each chapter is a short excerpt from the rather unfamiliar but hauntingly beautiful poetry of Sidney Lanier. These, alone, are almost worth the rather excessive price of the book.

Despite certain criticisms voiced above, it cannot be over-emphasized that this book is an achievement of great value and importance. Its author and the editor, Prof. Nicholas Polunin, are to be commended and congratulated. Ecology would be on a much sounder footing if comparable works were available for all the major ecosystems of the world. We look forward to the appearance of the companion work on the mangrove ecosystem.

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A PORTABLE, PICTURE FLORA FOR THE ALPS¹

This is one of the "Guides" published by the Swiss Alpine Club for the information, safety, and convenience

¹Landolt, E. 1960. *Unsere Alpenflora*. Verlag Schweizer Alpen-Club, Zollikon-Zürich. 220 + 72 pp., photographs in color. 19 SFr (\$4.40).

of its members and of mountaineering visitors to Switzerland. Most of the guides describe routes to the mountain huts and up and down the peaks. This guide has another mission, namely to make the pleasure of mountaineering more interesting. The book should give "an

introduction into the problems and relationships of the plant cover and the individual plants of the Alps with their environment and history plus some knowledge of how to recognize species." It succeeds beautifully.

The book is written for the layman. However, Latin names are used wherever critical data are given, and the indices allow ready translation of the few unaccompanied German vernacular names into the Latin (or into English or French vernacular names). Modern botanical concepts are used. For example, page 11, the first page of the section on the origin of the Alpine flora, introduces the ideas of flora, of vegetation, of the plant geographical basis for phylogeny, of pollen analysis of sediments and its ecological interpretation, of C^{14} age determinations of organic matter, of continental drift, etc. and uses them in constructing a picture of early Tertiary Swiss vegetation and its climatic and physiographic setting. This is a highly condensed book. It will be most instructive to plant taxonomists. Ecologists will also enjoy it of course.

Of the more than 1000 flowering plants that occur in the Swiss Alps above 1500 m elevation (subalpine belt in and above the spruce zone), about 300 are illustrated by photographs in color and a further 100 are briefly described and illustrated in black and white. A key of 18 pages using mostly flower colors and other easily recognized morphological features such as woody or herbaceous stems, opposite or alternate leaves, entire or cut leaves, etc. ends mostly with genera. It produces some odd concatenations such as the successive choices which key out Umbelliferae, *Allium schoenoprasum*, Androsace, and Primula. It does seem to be thoroughly workable. Many genera appear several times so one wrong choice is not always fatal to success. Grasses and sedges are not neglected.

A book such as this must be portable to be useful. Landolt's is. It weighs 239 g and has a volume of 244 cm³. For comparison, those interested in the flora of the Sierra Nevada of California must add to their usual field equipment a weight of 1700 g and a volume of 2165 cm³ when they use the splendid flora of California by Munz and Keck. Obviously the comparison is not fair since Munz and Keck include over 6000 species. Still, the standard field flora for Switzerland is not much bigger than the Club's guide to Alpine plants.

Actually, Landolt's book contains chapters on the origin of the Alpine flora, on the climate and soils of the Alps, on plants and their environments, on vegetation of the Alps, and on plant geography. Such information is not usual in identification manuals. The key, 106 pages of species descriptions, lists of literature, and full indices complete the book.

The plant descriptions deserve comment. Of the 4-5 lines devoted to a species, over half describes where the plant lives. The rest is on distinctive morphology. Unfortunately this admirable balance is not usual in floras even though keys can give most morphological information. The descriptions actually give height of the plant, characteristic morphological features, habitat, altitude, vegetation belt, soil (really soil parent material),

abundance, and geographical distribution over the entire range of the species.

The chapter on the history of the Alpine flora concentrates itself, as it should, progressively less from the present with man modifying the flora and vegetation so strongly, back through postglacial times, into the Pleistocene, and the Tertiary.

The chapter on climate and soils is a model of pertinent condensation. Principles illustrated by examples make climatic data condensable. Environmental relationships are illustrated by lists of nitrophilous, calciphilous, and calcifuge species. Vicarious species pairs on lime-rich and lime-poor substrates and between the eastern and western Alps are also tabulated.

The vegetation of the Alps is considered under altitudinal belts, with lists of characteristic species, and under plant communities. Vernacular as well as Latin names are used for the latter. In other words, the associations recognized by Braun-Blanquet and his colleagues are usable in describing vegetation for laymen. With the knowledge now available from plant sociological studies these descriptions are amazingly vivid. The lists of "frequent and typical" species for each association will aid plant identification since the *plant communities* are so well-described in habitat or ecological relationships, structure, and physiognomy as to be readily identifiable. The communities were originally defined floristically. This section on plant communities occupies only 15 pages, but it is a high point of the book. It illustrates the kinds of generalizations that can be made after long-continued study and the accumulation of much analyzed data.

The short chapter on plant geography details the floristic regions which have contributed plants to the flora of the Alps. The species entering into such elements are listed. Perhaps some of the discussion of geographical distribution could have been made more precise by adopting, or modifying, parts of Hultén's treatments of boreal floristics. Finally, there are plant geographical divisions within the Alpine flora itself "resulting from different geographical positions, different possibilities for glacial persistence, different distances from glacial age refugia, and different climatic and soil conditions." These differences are illustrated by the areas occupied by various localized species.

The color photographs form over a third of the bulk of the book. They concentrate on the plant being illustrated and not on the place where it lives. The photographs are arranged four or sometimes six to a page, but they do not seem crowded or excessively reduced in size. Scale varies from 2x to 1/10x life size, with the majority being about 1/2x. The colors are true; the plants appear natural; and the arrangement of single photographs on the pages is artistic, pleasing, and never monotonous although similar plants are placed together following the order which has been common in most floras.

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VASCULAR PLANTS OF SOUTHERN ILLINOIS¹

Illinois south of the 38th parallel is the area covered by this book. "Prepared for use by anyone having an interest in our native flora and who has had some introductory study of botany," the book provides an introduction listing characteristic plant species of twelve distinctive habitats, keys to and brief discussions of 1518 species, a two-page literature cited section, and a useful index listing every species even in small genera.

The keys are similar in general arrangement and in their employment of easily observable traits to those of Jones's *FLORA OF ILLINOIS* (1950. American Midl. Nat. Monogr. 5). Use of the keys in the field, however, is hampered by the lack of a glossary. Ten plates diagramming flower types, leaf shapes, structures of grasses, etc., would serve as a useful complement to a glossary

¹ Mohlenbrock, Robert H., and John W. Voigt. 1959. A flora of southern Illinois. Southern Illinois University Press, Carbondale. ix + 390 pp., 67 figs., 10 plates \$7.50.

but are no substitute for one. The discussions provided for most taxa include range, abundance, seasonal occurrence, and good descriptive information as to community or habitat occurrence. At least one specimen is cited for each taxon. Sixty-seven photographs of plants or vegetation are included, but several of these are unsuccessful because of small size, poor reproduction, or insufficient contrast in the original. Some, however, are excellent (e.g., Fig. 67 of *Ratibida pinnata* and Fig. 46 showing forest stratification).

For biologists in the area around the confluence of the Ohio and Mississippi Rivers, and especially for students of the still largely uninvestigated vegetation of southern Illinois, this flora will prove a workable, materially complete aid.

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THE ECOLOGY OF PLANT PATHOGENS¹

The study of plant pathology in the days when this reviewer was an undergraduate student was restricted, except possibly in very advanced courses, to the assimilation of information concerning the pathogen causing a disease, the signs and symptoms of such disease, and methods of control which had proven effective in the past. The thesis of the editors of these volumes is that there is more to the subject than this; if a person wants to become a plant pathologist, a doctor caring for plants and crops, he must know something about the pathogen whose action results in a diseased condition in the host plant, but more: he must have enough background to interpret the nature of the disease—abnormal plant physiology; the nature of the action of the pathogen on the host plant—pathogenicity, parasitism and fungitoxicity; and the nature of disease in large populations of crop plants—inoculum potential, spore dispersal, epidemiology, quarantine, cultural practices, chemical and biological interference with epidemics, and plant breeding for resistance.

To present the case for this type of exposition the editors have called on 47 persons from many parts of the world to present 41 of the 44 chapters in these books, while they have reserved for themselves the privilege of presenting an introductory chapter to each volume in which the scope of the volume is outlined both in relation to content and to its place in the series.

To introduce the series, the editors chose to explain what to them is plant pathology and the nature of plant disease. In contrast to human medicine, where the art of practice preceded the science of healing, in plant pathology the science of plant disease preceded the art of plant

healing or the application of scientific information to the health of plants. Disease is considered to be neither the condition nor the pathogen, each of which have given names to common diseases, but is taken to be a malfunctioning process resulting from the invasion of certain tissues by certain organisms or conditions. Considering disease as a process, six big processes are considered basic: "tissue is disintegrated; growth is affected; reproduction is affected; host is starved; water is deficient; respiration is altered." Following chapters on the scope and contributions of plant pathology, the history of plant pathology, and one answering the question 'how sick is the plant?', these six processes are each assigned one chapter. Plants are able to defend themselves against attack and this is brought out clearly in chapters on the histology of defense in plants, and on the physiology and biochemistry of defense. Types of hypersensitivity and predisposition to disease are considered as these subjects relate to the individual plant. Finally, Vol. 1 concludes with a chapter on therapy in which physical therapy, and topical and systemic chemotherapy are brought up to date from points of view of early and current work as well as of possibilities for future lines of attack. Thus Vol. 1 considers all phases of the diseased plant in relation to the organism or condition causing the disease condition.

¹ Horsfall, J. G. and A. E. Dimond, editors. 1959-60. Plant pathology; an advanced treatise. (symposium) Academic Press, Inc., New York & London. Vol. 1, The diseased plant. xiv + 674 pp., figs., \$22.00 (1959). Vol. 2. The pathogen. xiv + 715 pp., figs., \$22.00 (1960). Vol. 3, The diseased population, epidemics and control. xiii + 675 pp., figs., \$22.00 (1960).

Volume 2 is more interested in the pathogen. Animate, inanimate, and virus pathogens are considered. Three terms are clarified as follows: "The coexistence of two organisms is commensalism. If the commensalism is cooperative and both contribute to the food supply, we have symbiosis. If one partner supplies all the food and the other contributes nothing, we have parasitism. If one produces damage while it feeds, we have pathogenism." A brief discussion of the establishment of causality in disease is presented. Topics included in the second volume include an introductory chapter on the nature, origin, and evolution of parasitism in which it is shown that there is a continual development of the pathogen which enables it to parasitize plants in which certain

amounts of immunity have been developed. A chapter on the nature of virus multiplication is followed by a factual statement of the reproduction processes in bacteria, Actinomycetes and fungi. The morphology and physiology of spore germination is described in detail and this is followed by chapters on the physical and chemical abilities to breach host barriers. A detailed analysis is presented on the interaction of the pathogen, soil, other microorganisms in the soil, and the host. Fungi and bacteria produce toxins in plants and adjacent to roots and among these substances may be considered growth regulators including giberellins. Heterokaryosis, saltation and adaptation are important genetic aids to fungi and bacteria in their efforts to secure food supplies especially from host organisms which themselves have used genetic methods of combatting the pathogens. Passing from asexual to sexual organisms descriptions of three principal types of infective agents are presented in a discussion of the genetics of pathogenicity. Moving from growth and reproduction to control, the inactivation of viruses in culture and in living plants is described. The physiology of fungitoxicity is shown to be based on knowledge of cell structure and physiology. Chapters on fungicidal chemistry and nematocides complete the volume.

The third volume is devoted to what are called the public health aspects of plant pathology, the diseased population, epidemics and control. Again the editors' prologue acts as a guide for the volume in which inoculum potential and different methods of the dispersal of pathogens are emphasized. The author of the second chapter aptly quotes from the senior editor's earlier writings: "Hordes of soldiers will overrun almost any defense." This introduces a discussion of the inoculum potential in which it is shown that in most instances a limitless number of spores, amount of mycelium, or number of cells is required to produce an effective inoculum of a host whether in the laboratory, in nature, or in the field. The situation is rare in which a small number of cells or even one spore forms an adequate inoculum. In addition, weeds may carry disease-producing structures, and certain plants may carry disease but on them no symptoms are apparent. Autonomous dispersal, and dispersal of inoculum by insects and other animals, including man, are each given a prominent place in the volume. Many spores are dispersed by air and water. The discussion of the take-off of the spore from its parent cell, usually by violent discharge, is described, and for each type of take-off the discharge mechanisms are described and formulae describing the "sporabola" given. The physics of flight and landing of spores and other disseminules in the air and water are presented as a discussion of physical formulae describing the action of small bodies in air based on gravitation, velocity of fall, atmospheric turbulence, line of flight, range of flight, height of flight, duration of flight, concentration changes, problems of deposit, terminal velocity, impaction and precipitation effects. Epidemics are described by means of mathematical formulae. It is shown that the common concept of epidemics of plant disease: "there must be an aggressive parasite that multiplies fast, spreads far and swiftly, and is not particularly selective in its requirements" is a total misconception, by citing a number of plant disease epidemics and showing how their severity could be lessened both by pathological and agronomic practice. It is shown that in order to analyse and forecast epidemics of plant disease such information as the primary inoculum, its dispersal and transfer, the trapping of propagules by the host plant, infection, and the incubation period must

be known for each pathogen. The information thus obtained must be integrated and analysis may show that one or another of these stages in the development of the epidemic may not be important for a particular disease-producing organism. The economics of forecasting is discussed.

Problems in the area of plant quarantine are considered at length. Techniques of setting up a quarantine and making it effective are discussed. It is shown that where disseminules are air borne little can be done, but where diseased materials are transported by man from place to place, control by quarantine has been effected, and greater control can be effected in spite of apparent failure in some obvious instances. In a chapter on cultural practices in disease control it is shown how processes still in use in modern agriculture, developed from the earliest times, through refinement are being used and can be used to reduce plant disease. Soil treatment to control soil-borne disease is a problem in the ecology of soil populations as affected by chemical treatments used to eradicate or reduce the harmful effects of many kinds of bacterial, fungal and nematodal organisms without damage to the roots embedded in those soils. In a discussion of biological interference with epidemics, information is presented to show that use may be made of hyperparasites, phages, predators, antagonists, antibiotics and other methods used in the natural wars which proceed without end among the populations of organisms in the soil or above its surface. Finally, the series ends with a somewhat optimistic chapter showing how in spite of obvious failure in some cases, and in spite of the obstacles which must be surmounted, it is possible to breed into a host population resistance to attacks by pathogens even though the pathogen itself is continually breeding into its progeny the ability to attack the new varieties of host plants. But Stakman and Christensen add a note of warning and caution: "Intellectual horizons must continually be broadened, scientific skepticism must be maintained, and competent scientists must be given more adequate facilities than have ever been provided in the past. Plant diseases are indeed very "shifty enemies," and it would be fatal for scientists to repeat many of the mistakes, procedural and conceptual, of the past. Future progress should be much more rapid and substantial if full use is made of the lessons of the past."

The volumes are well bound, the type is clear, and there is a minimum of typographical error. In a very few places a sentence seems to have suffered from editing. Several chapters have been prepared by persons whose presentations might have been different in their native tongue than in English, but in only one instance does the text of the translation or transcription to English suffer. The quality of writing is high and each author has chosen illustrative material from his own area of interest. This leads to a certain amount of duplication, as would be expected, for if an attempt to weed out such repetition had been made individual treatments would have suffered and needless time would have been expended. Some chapters are in the nature of reviews of published material, others are based on known facts but explore the possibilities of application as being tried in current experimentation and future planning. The editors and publishers are to be congratulated in bringing together in three encyclopedic volumes this forward looking information on the disease of plants, its cause and prevention.

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STOCHASTIC POPULATION MODELS IN ECOLOGY¹

This book is an extension and summary of current work in the application of ecological models in which variance terms are explicitly retained.

It is a difficult but valuable book. It presents the first explicit ecological discussion of Monte Carlo methods and the first interesting use of an electronic computer for model evaluation.

Perhaps its prime value will be that statisticians or mathematicians who become interested in ecological problems (and for some fortunate and obscure reason the number of these people is increasing) can find here a clearly defined class of problems that is of biological interest and also of sufficient difficulty not to offend mathematical taste.

To have such a book is a great advance. It has been forty years and more since the work of Volterra made it obvious that mathematics and ecology would eventually fuse to their mutual benefit. A book completely embodying this fusion has yet to appear, but Bartlett has made an important beginning.

Kostitsyn, Volterra and Lotka have produced books that, I understand, are of some mathematical interest but as an ecologist I am not impressed with their applicability to what I consider the more interesting ecological problems.

¹ Bartlett, M. S., 1960. Stochastic population models in ecology and epidemiology. Methuen & Co., Ltd., London; John Wiley & Sons, Inc., New York (Methuen Monographs on Applied Probability and Statistics). x + 90 pp., 9 figs., 10 tables. \$2.00.

Several authors (including myself) have produced books on ecology in which mathematical concepts were used but mathematical elegance and rigor have been absent. This weakness has been due to both gaps in training and to the intractability of most ecological models.

Bartlett has tackled intrinsically interesting problems, such as the stability properties of populations and epidemics, has constructed appropriate models and at several points has checked out his results with experimental or observational data. Some of his models have surprising predictive power.

He makes it abundantly clear that purely deterministic models are of limited use in ecology. It seems possible, however, that even stochastic predictive theory will quickly hit against the awful diversity of species and will find itself solving endless collections of special problems which are of primary interest to a mathematician rather than an ecologist. It is significant in this connection that this is a Methuen Monograph on Applied Probability and Statics, not part of the Biology series.

I recommend it for biologists to read. It may be valuable. If it proves incomprehensible, send it as a gift to your favorite mathematician. The returns will probably be very high.

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 POLLEN ANALYSIS OF COASTAL Bogs FROM
CENTRAL ALASKA TO CALIFORNIA¹

The postglacial environments along a 2000-mile arc from Kodiak Island, Alaska, to northern California are described in terms of pollen stratigraphy and radiocarbon dating. This is a region of maritime climate and luxuriant forests; western hemlock, sitka spruce, mountain hemlock, lodgepole pine, and at lower latitudes western red cedar and coast redwood predominate. Heusser offers 78 new pollen diagrams; his discussion is based on these plus 36 previously published diagrams. Heusser's industry in the field is matched by an equally impressive laboratory record, approximately 2730 individual fossil extractions and, according to my calculation, over 400,000 pollen-spore determinations (not including *Sphagnum*).

By "Late Pleistocene" Heusser refers to the late-glacial and postglacial, roughly the last 14,000 years. The postglacial is subdivided according to the classic three-fold scheme of von Post, here identified as the early postglacial, hypsithermal, and late postglacial. Lodgepole pine pollen dominates the first interval; douglas fir

and oak characterize the the hypsithermal of coastal Washington with western hemlock and sitka spruce in southeastern Alaska; the late postglacial of coastal Washington is characterized by pine and a maximum of western hemlock, and in southeastern Alaska it features muskeg regeneration. 24 radiocarbon dates, virtually all lying at the bottom of the pollen profiles, provide excellent chronological control. As would be expected, the depth of organic sediments increases from north to south. There is no radiocarbon evidence that organic deposits in Oregon and Washington are older than those in coastal Alaska.

As their ability to recognize a greater variety of pollen-spore types increases, palynologists find increasing difficulty of reducing their diagrams to convenient size for publication. One is confronted with either costly and cumbersome fold-ins, with oversized pages, or with loss of legibility through overreduction. Heusser's is the latter fate. In accord with recent developments Heusser has paid careful attention to the NAP (Non-arboreal pollen, the herbaceous element). His inclusion of fern spores within the NAP sum raises the question of their ecological meaning, especially that of the Polypodiaceae. If we are to estimate relative degrees of tree density through the AP/NAP ratio, is it appropriate to include spores within the latter sum? Finally, one might ques-

¹ Heusser, Calvin J. 1960. Late-Pleistocene environments of North Pacific North America, an elaboration of late-glacial and postglacial climatic, physiographic, and biotic changes. American Geographical Society Special Publication No. 35, New York. xxiii + 308 pp., 25 plates, 48 figs., 10 tables, glossary. \$6.00 cloth, \$4.00 paper.

tion the basis of identifying species within those notoriously difficult genera, *Pinus* and *Picea*. Apparently Heusser has relied on a combination of pollen size statistics and on distributional assumptions.

The least secure of Heusser's conclusions is his claim of a Late-glacial sequence, comparable to that of Europe and eastern North America. In these areas the record of late-glacial and full-glacial pollen rains, and of ice-margin vegetation, has come largely from inorganic sediments. To obtain abundant pollen from such material one must employ either hydrofluoric acid digestion, flotation, or some other means of reducing mineral content. By restricting his study to organic sediments and by using only

KOH in extraction, it is quite unlikely that Heusser has captured the late-glacial record. Although five of his C-14 dates are older than 10,000 years, none exceed 11,000, the time when severe ice margin conditions and a periglacial flora very different from that he has so abundantly recorded for the postglacial would be expected. Within the postglacial period we can accept Heusser's study with greater confidence; it is a masterful piece of work equal to the vastness of the North Pacific.

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TWO TERTIARY FLORAS¹

The two fossil floras furnishing the subject matter for these papers are both found in the Tertiary lake deposits of the upper Ruby River Basin in southwestern Montana, 70-80 miles northwest of West Yellowstone. Although the two localities are separated by only 1½ to 3 miles, the floras are markedly different in composition and aspect. The field work extended over a period of more than ten years. The fossils of Oligocene age (1961) are very sparsely distributed in the enclosing shales and require the working over of a great amount of material. Dr. Becker is to be admired for the amount of energy and physical labor expended in accumulating his rather extensive collection. The Ruby flora comprises 82 determined species distributed in 61 genera. The writer is to be commended on an excellent, if rather brief, account of the regional geology, local flora, and fossil flora, together with considerations of the age and ecological aspects of the fossil plants. The illustrations are well done and show the fine preservation of the material. The taxonomy is careful and accurate and is clearly the result of much painstaking herbarium and museum research. The author may wish to make a few changes in identifications and synonymies. For example, *Myrica dorfi* Becker is probably not a *Myrica* but an alder related to the *Alnus relata* (Knowlton) Brown complex; compare plate 12, figures, 3 and 4, with plate 14, figures 1-15 and plate 15, figure 1. Plate 13, figure 1, *Populus balsamoides* Goepfert is repeated in the Mormon Creek paper as plate 26, figures 3 and 9. The Ruby flora *Cercidiphyllum* is not *C. elongatum* Brown, at least it is not the same species as that in the Lower Eocene Chalk Bluffs flora of California. There is some confusion in the nomenclature of the Tertiary species of *Cercidiphyllum* and the synonymies should be restudied and revised. At the Ruby locality is found the second occurrence of the extinct *Fagopsis longifolia* (Lesquereux) Hollick, previously known only from Florissant, Colorado. There is the same association of typical leaves and deciduous cone scales. The family status of this fossil form must still remain in doubt. Dr. Leopold (p.

60) found fagaceous pollen by treating material scraped from one of the Florissant fossil cones, but we cannot be sure that this pollen was borne by the particular cone; it could have lodged among the cone scales during deposition of the Florissant shales.

The Ruby flora is a derivative of the Florissant flora with 40% of species, and approximately 60% of genera, in common with the older flora. It contains many of the characteristic Florissant species such as: *Chamaecyparis linguafolia* (Lesquereux) MacGinitie, *Populus crassa* (Lesquereux) Cockerell, *Fagopsis longifolia* (Lesquereux) Hollick, *Morus symmetrica* Cockerell, *Mahonia obliqua* MacGinitie, *Astronium truncatum* (Lesquereux) MacGinitie, *Cardiospermum terminale* (Lesquereux) MacGinitie and *Philadelphus parvulus* Becker. In the interval of 8 million years or more between the Florissant and the Ruby floras some of the more tropical-appearing genera (*Athyana*, *Bursera*, *Caesalpinites*, *Eugenia*, *Persea*, *Petrea*, *Thouinia* and *Trichilia*) seem to have been eliminated and instead we find in the younger flora about a half dozen genera of temperate aspect which now live in the general area; *Alnus*, *Betula*, *Chamaebatia*, *Potentilla*, *Spiraea* and *Symphoricarpos*. There are 10 species of Rosaceae in the Ruby flora but only one of Leguminosae, as contrasted to 11 and 10 respectively in the Florissant. There are some genera curiously absent from the Ruby flora: *Carya*, *Juglans*, *Liquidambar*, *Platanus*, *Rhus*, *Robinia* and *Tilia* for example. Their absence may be due to chances of preservation and collecting and they may be found in later studies of the pollen flora.

The sequence of floras—Green River, Florissant, Ruby, and Kilgore—form a series of points on the continuum of floristic evolution in the general area; points in space as well as time. In all these floras there recur definite indications of subhumid conditions on the interfluvies. In the Ruby flora Dr. Becker designates as a xeric element the oaks with non-lobed leaves, *Cardiospermum*, *Cercocarpus*, *Cotinus*, *Dodonea*, *Mahonia*, *Ribes* and the like. (p. 29.). This same group appears in the Florissant together with pollen and megafossils of *Ephedra*. We might question the author's use of the word "desert" (p. 34) in this connection since the term subhumid would be more applicable. Just how far adaptations to xeric conditions had progressed by the Late Oligocene or Lower Miocene we cannot exactly say, neither can we be absolutely sure that the adaptations of this group of plants in the late Oligocene was the

¹ Becker, Herman F. 1960. The Tertiary Mormon Creek Flora from the upper Ruby River Basin in southwestern Montana. *Paleontographica*, Abt. B, vol. 107, pp. 83-126. 35 plates, 3 figs., 8 tables. Stuttgart.

Becker, Herman F. 1961. Oligocene plants from the upper Ruby River basin, southwestern Montana. *Geological Society of America, Memoir* 82, pp. 1-127. 32 plates, 8 tables. New York.

same as it is today. There seems to have been time enough, 10-15 million years, between the flora of the Green River and that of the Ruby basin for the processes of genetic change and natural selection to have achieved a rather complete adaptation to subhumid or even desert habitats. There is at least one clear instance of such an adaptive change. In the Florissant flora is a large-leaved mountain mahogany (*Cercocarpus myricaeifolius* (Lesquereux) MacGinitie) which was obviously a member of the moist-ground, stream-side flora. This is indicated by the presence of abundant leaves of the species associated with the leaves of such genera as *Chamaecyparis*, *Populus*, *Sequoia*, *Typha* and *Zelkova*, at every locality of the flora. By the time of deposition of the Ruby shales the *Cercocarpus* leaves (pl. 22, figs. 2-6) had been reduced in size to those of the living, dry-ground species. The author includes *Dipteronia* as one of the subhumid genera (pp. 26-29), this is an error.

The reviewer would take issue with the author concerning his emphasis on floral migration in explaining certain flora relationships. It is extremely doubtful that "migrations" of floras as entities occurred during the Tertiary. Floristic change and evolution were going on all the time over the whole area. New species were arising, others becoming extinct; new species were dispersing into and across the area and others dispersing out of the area. (See Mason.²) In the reviewer's opinion continuous floristic evolution in any region, rather than migrations from centers of dispersal, best explains the distribution of fossil plants. The Ruby flora resembles the Florissant flora since it represents a later stage of floristic evolution in the area, not because the two localities were connected by a "pathway of migration" (p. 34).

Dr. Becker has arrived at the most probable age of the flora as late Oligocene and this seems as accurate an age estimate as it is possible to make. Approximately 30 or 52% of the genera are now living in the general floristic region, which would place the age of the flora as late Miocene according to the curve of Wolfe and Barghoorn³ (p. 395), a conclusion not acceptable to the reviewer. Dr. Becker is to be complimented on the excellence of this, his second monograph in the field of paleobotany.

The other paper under review, the Mormon Creek flora, is not up to the standard of quality achieved in the paper on the Ruby flora. The preservation of the Mormon Creek fossils is considerably inferior to those

at the Ruby locality and this increases the difficulties of identification and correlation. A botanist would scarcely consider identifying a few fragments of leaves with two or three similar fragments from a species growing a thousand miles distant, yet paleobotanists seem addicted to this practice (the reviewer is guilty), although the results should not be taken too seriously. In the case of the Mormon Creek flora the practice has resulted in an apparent correlation with the Wilcox and Chalk Bluffs floras and a late Lower Eocene age assigned to the flora. However, if the species correlations are critically examined it is seen that many of them are of doubtful validity and any age relationship established thereby open to serious question. The reviewer believes that this flora cannot be older than late Green River age, and it may be considerably younger. There are 51 species of angiosperms, 38 of which have non-entire leaves, a proportion not at all characteristic of Lower or Middle Tertiary floras.

Dorf has published a list of species from the Yellowstone Park Floras⁴ whose age is placed in the interval late Lower Eocene—early Middle Eocene. Although the Yellowstone Park localities are within 100 miles of the Mormon Creek locality, and according to the author of nearly the same age, yet there are only three species in common, and there is reasonable doubt concerning the correct identification of two of these. Since the Yellowstone and Mormon Creek flora are so near each other, if they were of approximately the same age there should be a large number of species in common. In contrast to this 40% of the Ruby species are found in the Florissant flora which is somewhat older and about 550 miles distant.

The identification of several of the Mormon Creek species needs revision. *Myrica lignitum* (pl. 27, figs. 7, 8) is founded on leaflets and is probably assignable to *Rhus*; *Myrica mormonensis* (pl. 27, figs. 16-20) is also founded on leaflets; the *Quercus elwyni* (pl. 28, figs. 1-7) leaves are rosaceous and probably assignable to *Crataegus*; the *Cercidiphyllum* (pl. 29, figs. 1-6) does not appear to be the same as the Chalk Bluffs species; *Cassia glenni* (pl. 30, fig. 8) is of doubtful validity; *Ilex rubyensis* (pl. 31, figs. 6-9) is founded on what are doubtless leaflets, not leaves. These examples are chosen at random; there are others. It is regrettable that the author did not give himself more time for consideration of this difficult flora before publishing the paper; and it is to be hoped that he will publish a thorough revision in the near future.

H. D. MACGINITIE

PROFESSOR EMERITUS

CALIFORNIA STATE COLLEGE SYSTEM

⁴ Dorf, Erling, 1960. Tertiary fossil forests of Yellowstone National Park. Billings, Montana. Geol. Soc. 11th Field Conference, pp. 253-257.

ERRATUM

In Ecology for April 1961, Vol. 42, No. 2, in the article by D. A. Crossley, Jr. and Henry F. Howden, "Insect-Vegetation Relationships in an Area Contaminated by

Radioactive Wastes" on page 309 the legends for figures 5 and 6 should be reversed.

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